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FLORA OF PANAMA

BY

ROBERT E. WOODSON, JR.

AND

ROBERT W. SCHERY

AND COLLABORATORS

PART IV

Fascicle 4

CHENOPODIACEAE (J. A. Duke)
AMARANTHACEAE (J. A. Duke)
NYCTAGINACEAE
BATIDACEAE
PHYTOLACCACEAE (K. Raeder)
AIZOACEAE (L. I. Nevling, Jr.)
PORTULACACEAE (L. I. Nevling, Jr.)
CARYOPHYLLACEAE (J. A. Duke)

ANNALS
OF THE
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Vol. XLVIII FEBRUARY, 1961 No. 1

FLORA OF PANAMA

Part IV. Fascicle 4*

CHENOPODIACEAE

By JAMES A. DUKE

Flowers perfect or unisexual, monoecious, polygamous or dioecious, sessile or shortly pedicellate, often bracteate and bibracteolate, the bracts mostly herbaceous. Perianth uniseriate, of (0–) 2–5 lobes, usually hypogynous, the lobes discrete or basally connate, usually greenish. Corolla absent. Stamens as many as or fewer than the sepals, the filaments mostly discrete, the anthers 2–4-locellate, usually introrse and dorso-medially attached. Ovary superior, unilocular, uniovulate, the ovule erect on a short funicle or pendulous from an elongate funicle; styles 1–3, the stigmata capitate or elongate or the stigmata 2–5 and elongate. Fruit a 1-seeded indehiscent or circumscissile utricle, the perianth often and the sepals occasionally adherent to the seed; seeds erect, horizontal or inverted, lenticular, cochleate, subglobose or ellipsoid; embryos circular or hippocrepiform and more or less encircling the endosperm or spirally coiled and nearly filling the seed. Herbs, rarely shrubs or small trees, with simple alternate or opposite exstipulate leaves, these often farinose or glandular. Flowers glomerulate in axillary or terminal spikes, racemes, panicles or cymes, or rarely solitary and axillary, or embedded in the strobiloid axis of the inflorescence.

Embracing about a hundred genera and more than a thousand species, the chenopods are a rather cosmopolitan family containing many weeds and halophytes in addition to a few vegetables such as the beet, spinach and swiss chard, the first of which is sometimes grown around the Canal Zone. Three weedy species of *Chenopodium* occur in Panama, one probably native, the other two known only as weedy advents on San Jose Island.

1. CHENOPODIUM L.

CHENOPODIUM L. Sp. Pl. 218. 1753.
Morocarpus Adans. Fam. 2:261. 1763.
Anserina Dumort. Fl. Belg. 21. 1827.
Teloxys Moq. in Ann. Sci. Nat. 2^1:289. 1834.

* Assisted by a grant from The National Science Foundation.

Issued April 3, 1961.

Agathophytum Moq. loc. cit. 2[1]:291. 1834.
Roubieva Moq. loc. cit. 2[1]:292. 1834.
Oligandra Less. in Linnaea 9:199. 1834. non *Oligandra* Less. 1832.
Orthosporum T. Ness, Gen. Fl. Germ. Dicot. 1: *pl. 57*. 1835.
Ambrina Spach, Hist. Veg. 5:295. 1836.
Botrydium Spach, loc. cit. 5:298. 1836.
Lipandra Moq. Chenop. Enum. 19. 1840.
Gandriloa Steud. Nom. Bot. 2[1]:662. 1840.
Oliganthera Endl. Gen. 1377. 1841.
Oxybasis Kar. & Kir. in Bull. Soc. Nat. Mosc. 1841:738. 1841.
Orthospermum Opiz, Seznam 70. 1852.
Vulvaria Bubani, Fl. Pyren. 1:174. 1897.
Botrys Nieuwl. in Am. Midl. Nat. 3:274. 1914.

Flowers perfect or rarely unisexual, sessile or subsessile, ebracteate. Sepals (3–) 5, hypogynous, free or basally united, herbaceous, subequal, often strongly 1-ribbed and cucullate. Stamens 5 or fewer, occasionally varying in number in different flowers of the same inflorescence, the flattened filaments free or basally connate, the anthers mostly suborbicular, introrse, dorso-medially attached. Ovary subglobose, the stigmata 2 (–5), filiform or subulate, mostly sessile or subsessile. Fruit an indehiscent utricle, ovoid to subglobose, the pericarp membranaceous to carnose, free or adherent to the single seed; seeds mostly cochleate-lenticular, smooth to roughened, vertically or horizontally oriented. Annual or perennial often strong-scented herbs. Leaves alternate, entire to pinnatifid, the lowermost at least usually petiolate, frequently glandular or farinose. Inflorescences of terminal or axillary glomerules, the glomerules variously arranged.

Consisting of about a hundred weedy species, *Chenopodium* is a rather cosmopolitan assemblage of meager economic importance. Various species are used in Central America and elsewhere as potherbs, condiments and vermifuges. Three easily differentiated species are presently known to occur in Panama, but several others occur in Central America north of Panama.

a. Plants farinose, never with oil glands on the leaves and inflorescence; seeds horizontal, dull or lustrous, 1–1.5 mm. broad, the circular embryo completely encircling the endosperm.

  b. Leaf blades rhombic, dentate; sepals merely 1-ribbed; seeds dull, tuberculate, 1.2–1.5 mm. broad, the margins acute; pericarp adherent to the seeds..... 1. C. MURALE

  bb. Leaf blades lance-linear to oblong, entire; sepals carinate; seeds lustrous, smooth, 1–1.2 mm. broad, the margins obtuse; pericarp free of the seeds..... 2. C. PRATERICOLA

aa. Plants glandular, with resinous dots on the leaves and inflorescence; seeds horizontal and vertical, lustrous, 0.6–0.8 mm. broad, the hippocrepiform embryo incompletely encircling the endosperm..... 3. C. AMBROSIOIDES

1. CHENOPODIUM MURALE L. Sp. Pl. 219. 1753.

Atriplex muralis Crantz, Inst. 1:206. 1766.
Chenopodium guineense Jacq. Coll. 2:346. 1788.
Chenopodium carthagenense Zuccagni, in Roem. Coll. 133. 1806.
Chenopodium murale β *albescens* Moq. Chenopod. Enum. 32. 1840.
Chenopodium murale γ *carthagenense* Moq. loc. cit. 32. 1840.

Vulvaria trachiosperma Bubani, Fl. Pyren. 1:177. 1897.
Chenopodium murale spissidentatum Murr, in Magyar Bot. Lap. 2:11. 1903.

Erect or ascending annuals to as much as 6 dm. tall, the branches ascending, often deeply sulcate, occasionally farinose, especially toward the extremities. Leaves somewhat lustrous and occasionally bullate above, glabrous to rather densely farinose below, deltoid to rhomb-ovate, marginally irregularly and acutely dentate, apically acuminate to attenuate and often mucronate, basally acute to truncate, 2.5–8 cm. long, 2–5 cm. broad, the petioles mostly 3–70 mm. long, sometimes quite as long as the blades. Flowers irregularly disposed in glomerules, the glomerules sessile along the dichotomously branching rhachises, these axillary and terminal, distally farinose. Sepals 5, subequal, ovate, obtuse, cucullate, 1-ribbed, slightly if at all carinate, farinose, basally connate, 1–1.5 mm. long; stamens 5, caducous, the filaments flattened, the anthers orbicular, exserted; ovary subglobose, the style quite short, the 2 (–3) stigmata ca. twice as long, spreading, irregularly glandular. Utricle partially enclosed by the sepals, the seed lenticular-cochleate, minutely tuberculate, dull reddish-brown, 1.2–1.5 mm. broad, horizontal, the pericarp adherent.

Presumably a native of Europe, Asia and Africa, now widely adventive in America as far north as Canada; in Panama known only as a lawn weed in San Jose Island.

PANAMÁ: main camp, San José Island, Perlas Archipelago, Gulf of Panama, ca. 55 mi. sse. of Balboa, *Johnston 1206*.

2. CHENOPODIUM PRATERICOLA Rydb. in Bull. Torr. Club 39:310. 1912.

Chenopodium petiolare var. *leptophylloides* Murr. in Bull. Herb. Boiss. 2^4:994. 1904.
Chenopodium leptophyllum var. *leptophylloides* Thellung & Aellen, in Fedde, Rep. Spec. Nov. 26:134. 1929.
Chenopodium pratericola var. *leptophylloides* Aellen, in Ostenia 100. 1933.
Chenopodium pratericola ssp. *pratericola* var. *leptophylloides* Aellen, in Am. Midl. Nat. 30: 64. 1943.

Erect or ascending annuals to as much as 3 dm. high, the branches ascending, usually multisulcate, bicolored, bullate or farinose, especially distally. Leaves yellowish-green above, whitish and densely farinose below, narrowly oblong to lanceolate, entire or rarely subhastatulate, apically obtuse to acute and mucronulate, basally acute to attenuate, 10–45 mm. long, 2–10 mm. broad, the petioles 2–10 mm. long. Flowers sessile in dense glomerules, the glomerules in panicled interrupted spikes, the rhachises densely farinose. Sepals 5, subequal, ovate, subacute, cucullate, strongly carinate, farinose, basally connate, ca. 1 mm. long; stamens 5, the flattened filaments included, the anthers orbicular; ovary subglobose, the 2 stigmata sessile or subsessile, spreading, irregularly glandular. Utricle completely embraced by the sepals, the seed lenticular-cochleate, smooth, lustrous, reddish-brown, 1–1.2 mm. broad, horizontal, loosely embraced by the pericarp.

Western United States to Mexico; Argentina; probably adventive on San Jose Island as it is in the eastern United States.

Fig. 110. *Chenopodium pratericola*

PANAMÁ: abandoned corral, San José Island, Perlas Archipelago, Gulf of Panama, ca. 55 mi. sse. of Balboa, *Johnston 1230.*

The occurrence of this species as a weed on San Jose Island would tend to substantiate I. M. Johnston's claim (in Sargentia 8:30. 1949) that the weeds were introduced from Texas in unclean hay. The two related taxa [*C. pratericola* ssp. *pratericola* var. *thellungianum* Aellen, with linear leaves, and *C. pratericola* ssp. *desiccatum* (A. Nelson) Aellen, a semi-prostrate form] were unknown in Texas at the time of Aellen's monograph (in Fedde, Rep. Spec. Nov. 26:119. 1929). It must be noted that Aellen (in Am. Midl. Nat. 30:64. 1943) has reduced *C. dessiccatum* to a subspecies of *C. pratericola*, a very peculiar mishap since *C. desiccatum* antedates *C. pratericola* by 10 years and seems not to be homonymous. If they do indeed prove to be mere subspecies of the same species, several new combinations will be required, but I will leave these for the monographer.

3. CHENOPODIUM AMBROSIOIDES L. Sp. Pl. 219. 1753.

Chenopodium anthelminticum L. Sp. Pl. 220. 1753.
Atriplex ambrosioides Crantz, Inst. 1:207. 1766.
Atriplex anthelmintica Crantz, loc. cit. 1:207. 1766.
Chenopodium suffruticosum Willd. Enum. 290. 1809.
Chenopodium spathulatum Sieber, Fl. Martin. 92. 1825.
Chenopodium santa-maria Vell. Fl. Flum. 126. 1825.
Chenopodium chilense Schrad. Ind. Sem. Hort. Gotting. 1832:2. 1832. non Pers. 1805.
Orthosporum ambrosioides Kostel. Allg. Med.-Pharm. Fl. 1433. 1835.
Orthosporum suffruticosum Kostel. loc. cit. 1433. 1835.
Ambrina chilensis Spach, Hist. Veg. 5:297. 1836.
Ambrina ambrosioides Spach, loc. cit. 5:297. 1836.
Ambrina anthelmintica Spach, loc. cit. 5:298. 1836.
Roubieva anthelmintica H. & A. Bot. Beech. Voy. 387. 1840.
Chenopodium retusum Juss. ex Moq. in DC. Prodr. 13^2:73. 1849.
Chenopodium obovatum Moq. loc. cit. 13^2:73. 1849.
Ambrina denudata Phil. in Linnaea 29:37. 1856.
Chenopodium ambrosioides anthelminticum A. Gray, Manual 2:364. 1856.
Ambrina andicola Phil. in Anal. Univ. Sant. 91:442. 1895.
Chenopodium querciforme Murr, in Mag. Bot. Lap. 3:37. 1904.
Blitum ambrosioides G. Beck, in Reichenb. Ic. Fl. Germ. 24:118. 1908.
Botrys ambrosioides Nieuwl. in Am. Midl. Nat. 3:275. 1914.
Botrys anthelmintica Nieuwl. loc. cit. 3:275. 1914.
Chenopodium vagans Standl. in N. Am. Fl. 21:26. 1916.
Also numerous other infraspecific names; see Aellen (in Am. Midl. Nat. 30:51. 1943).

Erect or ascending ill-scented perennials to as much as 15 dm. high, the branches ascending, usually multisulcate, bicolored, often lignescent, glabrous to tomentulose or villose about the inflorescence. Leaves yellowish green, puberulent, villosulous or glabrate, glandular, with amber-colored secretions, lanceolate to rhomb-elliptic, entire to coarsely and irregularly sinuate-dentate or sinuate-pinnatifid, apically acute, basally attenuate, 2–12.5 cm. long, 0.5–5.5 cm. broad. Flowers sessile, usually in dense glomerules, these contiguous or not and paniculately disposed, interspersed with reduced or rather large leaves, the rhachises glandular and villosulous to glabrate. Sepals (3–) 5, subequal, narrowly ovate, cucullate, very slightly carinate if at all, connate for about one third their length,

ca. 1 mm. long; stamens (3–) 5, the flattened filaments about as long as the sepals, the anthers orbicular, slightly exserted; ovary subglobose, the sessile or subsessile stigmata spreading, irregularly glandular. Utricle completely embraced by the sepals, the seed lenticular-cochleate, smooth, lustrous, reddish-brown, 0.6–0.8 mm. broad, horizontal and vertical, loosely embraced by the pericarp.

A cosmopolitan weed, perhaps indigenous in Mexico and Central America.

CHIRIQUÍ: Alto Lino, 4200 ft., *Bro. Maurice 882*. PANAMÁ: Juan Díaz, *Standley 30529*.

Polymorphically perplexing, this species, or some of its subspecies, varieties or forms, is quite cosmopolitan. Colloquial names applied to the wormseed in Central America are almost as numerous as the Latin names. In Panama only the name "paico" has been encountered. The plant is used medicinally as a vermifuge, a poultice and reputedly even as a soporific; it is also used as a culinary flavoring.

AMARANTHACEAE

By JAMES A. DUKE

Flowers perfect or unisexual, monoecious, polygamous or dioecious, mostly pentamerous, usually bracteate and bibracteolate, sessile or short-pedicellate. Calyx uniseriate or biseriate, commonly hypogynous; sepals (2–) 5, discrete or partially connate, scariose, whitish or variously colored. Corolla absent. Stamens (2–) 5, rarely more, hypogynous or perigynous, the filaments discrete or flattened and united below into a tube, the tube often with filamentous pseudostaminodia inserted between the filaments; anthers 2- to 4-locellate, usually introrse and dorso-medially attached. Ovary superior, unilocular, uniovulate (multiovulate in *Pleuropetalum, Celosia* and allied genera); ovules campylotropous on mostly elongate flattened funicles; styles 1–8; stigmata capitate or filiform. Fruit a 1-seeded utricle or rarely a several-seeded capsule, often circumscissile; seeds usually cochleate-orbiculate, the embryo excentric in a mealy endosperm. Herbs, shrubs, small trees or clambering vines with alternate or opposite mostly entire exstipulate leaves. Inflorescences of solitary flowers, spikes, glomes, glomerules, or thyrses simply, racemosely or corymbosely disposed.

This largely tropical and subtropical family, of some 50 genera and 500 species, is represented in Panama by eleven of the twelve genera thus far reported for Central America. The twelfth genus, represented in Central America by *Froelichia interrupta*, has not yet been reported between Guatemala and Colombia. Many of the Panama species are cultivants or anthropochorous weeds of disturbed habitats. Several species in several genera are employed as potherbs and species of *Amaranthus* are a source of grain. Species of *Iresine, Celosia, Amaranthus* and *Gomphrena* are planted as ornamentals in Central America and other places.

a. Leaves alternate; fruit a many-seeded capsule or a 1-seeded utricle; stigmata 2–8; anthers 4-locellate.
  b. Fruit a many-seeded capsule; stamens united below for nearly half their length; stigmata 2–8, usually exceeding the calyx.
    c. Capsules exceeding the usually deflexed sepals; seeds more than 10; stigmata 2–8, as long as or longer than the sulcate style; inflorescence paniculate or corymbose; leaves usually ovate; woodland plants..... 1. PLEUROPETALUM
    cc. Capsules included by the erect sepals; seeds less than 10, stigmata 2–3, much shorter than the terete style; inflorescences of mostly simple spikes (very complex fasciated inflorescences in cultivants); leaves mostly lanceolate; cultivants or escapes (in Panama)..... 2. CELOSIA
  bb. Fruit a 1-seeded utricle; stamens discrete or united below for less than a third of their length; stigmata 2–3, exserted or included.
    d. Flowers monoecious or polygamo-monoecious (in Panama spp.); filaments discrete; seeds exarillate, reddish brown, less than 1.5 mm. broad; erect or ascending herbs..... 3. AMARANTHUS
    dd. Flowers perfect; filaments basally connate; seeds arillate, black, 1.5–2.5 mm. broad; clambering suffruticose herbs or shrubs..... 4. CHAMISSOA
aa. Leaves opposite; fruit a 1-seeded indehiscent utricle; stigmata 1–3; anthers 2- to 4-locellate.
  e. Inflorescences of elongate spikes, the constituent flowers or glomerules deflexed in fruit; bracts and bracteoles strongly spinescent; anthers 4-locellate; style 1, with a capitate stigma.
    f. Flowers not glomerulate, perfect; spines straight or slightly arcuate; seeds 0.8–1.2 mm. broad, reddish brown; sepals glabrate or minutely tomentose, without protrusive ribs..... 5. ACHYRANTHES
    ff. Flowers glomerulate, some sterile and highly modified; spines uncinate; seeds 1–2.5 mm. broad, succineous; sepals pilose, with strongly protrusive ribs..... 6. CYATHULA
  ee. Inflorescences of panicles, racemes, glomerules or short congested spikes, the constituent flowers not strongly deflexed in fruit; bracts rarely spinescent (*Alternanthera* spp.); anthers 2-locellate; styles 1–3, the stigmata filiform, cylindric or capitate.
    g. Inflorescences of spikes in much branched panicles (in Panama); flowers perfect, polygamous or dioecious, often with an obvious tuft of hairs arising between the bracts and sepals; stigmata 1–3, if 1, bilabiate; erect herbs, shrubs, trees or clambering vines.
      h. Flowers perfect; stigma 1, bilabiate; outer 3 sepals much broader than the inner, with the basal hairs borne mostly inside the outer sepals; clambering suffruticose perennials..... 7. PFAFFIA
      hh. Flowers perfect or dioecious; stigmata 2–3, filiform to deltoid; sepals subequal, the basal hairs arising mostly outside the sepals; erect herbs or shrubs (in Panama)..... 8. IRESINE
    gg. Inflorescences of spikes or glomes, these solitary or in trichotomously few-branched corymbs; flowers perfect; tufts of intrafloral hairs not obvious to the naked eye; stigmata 1–2, if 1, capitate; procumbent or erect herbs (*Alternanthera* spp. may be shrubby clamberers).
      i. Leaf bases amplexicaul, with a tuft of short hairs around the cupuliform node; stigmata 2; pseudostaminodia absent, the filament tube short or absent; flowers short-pedicellate within the bracteoles..... 9. PHILOXERUS
      ii. Leaf bases not amplexicaul, thus not forming a cup with a tuft of hairs around the node; pseudostaminodia well-developed (in Panama), the filament tube obvious; flowers sessile within the bracteoles.
        j. Stigma 1, capitate to short-cylindric; anthers with an obvious filament inserted between the lacerate or dentate pseudostaminodia; bracteoles shorter than the sepals, not conspicuously cristate (in Panama)..... 10. ALTERNANTHERA
        jj. Stigmata 2, filiform; anthers sessile at the summit of the filament tube between bilobate pseudostaminodia; bracteoles equaling or exceeding the sepals, cristate..... 11. GOMPHRENA

Fig. 111. *Pleuropetalum pleiogynum*

1. PLEUROPETALUM Hook. f.

PLEUROPETALUM Hook. f. in Proc. Linn. Soc. 1:278, and in Lond. Jour. Bot. 5: 108. 1846.

Allochlamys Moq. in DC. Prodr. 13²:463. 1849.
Melanocarpum Hook. f. in Benth. & Hook. Gen. 3:24. 1880.

Flowers perfect, subsessile to pedicellate, unibracteate and bibracteolate. Sepals 5, discrete, hypogynous, concave, subequal, many-ribbed. Petals absent. Stamens 5–8, hypogynous, connate about half their length forming an exappendiculate tube shorter than the ovary; filaments flattened; anthers 4-locellate, introrse, medially attached. Ovary subglobose, 1-locular, multi-ovulate; ovules campylotropous; funicles flattened or filiform, exarillate, with free central placentation; style 1; stigmata mostly 3–6, at anthesis scarcely distinguishable, ultimately reflexed. Fruits at first baccate, later developing into circumscissile or irregularly dehiscent capsules; seeds cochleate-orbiculate, black, lustrous, reticulate. Glabrate sparingly branched erect suffruticose herbs or shrubs. Leaves alternate, entire, petiolate, lanceolate to rhombic-ovate, glabrous to minutely strigillose, deciduous. Inflorescences of terminal and axillary racemes, panicles or corymbs, with or without foliar leaves.

Inhabiting moist forests of low elevations, this genus, of perhaps three species, ranges from Jalisco to Peru and the Galapagos Islands. The type species, *P. darwinii* Hook. f., endemic to the Galapagos Islands, was reluctantly assigned to the Portulacaceae by Bentham & Hooker (Gen. 1:157. 1862.). The two other species of this economically unimportant genus are both found in Panama.

a. Inflorescence corymbose; sepals with 7–17 ribs; stigmata mostly 3–4; capsule irregularly dehiscent; seeds 1.5–2.2 mm. broad..... 1. P. SPRUCEI
aa. Inflorescence racemose or paniculate; sepals with 19–27 ribs; stigmata mostly 5–7; capsule circumscissile; seeds 1–1.5 mm. broad..... 2. P. PLEIOGYNUM

1. PLEUROPETALUM SPRUCEI (Hook. f.) Standl. in N. Am. Fl. 21:96. 1917.

Melanocarpum sprucei Hook. f. in Benth. & Hook. Gen. 3:24. 1880.
Pleuropetalum costaricense Hort. Kew, ex Hemsl. Biol. Centr. Am. Bot. 3:12. 1882.
Pleuropetalum tucurriquense Donn. Smith, in Bot. Gaz. 61:387. 1916.
Pleuropetalum calospermum Standl. in Jour. Wash. Acad. Sci. 13:368. 1923.

Erect sparingly branched subglabrous suffruticose herbs or shrubs to 3 m. high. Leaves glabrous to minutely strigillose on the veins below, broadly lanceolate to rhombic-ovate, often falcate, apically attenuate, basally acute to subrounded, 3–15 cm. long, 1–6 cm. broad; petioles 5–20 mm. long. Inflorescences of mostly terminal corymbose racemes, the rhachises usually glandular. Flowers perfect, on pedicels 1–10 mm. long; bracts and bracteoles subequal, ovate to orbicular, carinate, 0.5–1 mm. long; sepals 5, subequal, ovate, concave, glabrate or scurfy, rounded to subacute, ultimately spreading, 2–4 mm. long, 1–2 mm. broad, with 7–13 (–17) ribs; stamens 5–8; filaments 2–3 mm. long; filament tube 1–2 mm. long; anthers oblong; ovary globose; style 1, about 0.5 mm. long; stigmata mostly 3–4, longer than the style, ultimately reflexed. Fruit an irregularly dehiscent capsule exceeding

the sepals, 4–7 mm. long, 3–6 mm. broad; seeds cochleate-orbiculate, black, lustrous, reticulate, 1.5–2.2 mm. long, on filiform or flattened funicles becoming 1–3 mm. long.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1028*. CHIRIQUÍ: Bajo Mono, Boquete District, 4500 ft., *Davidson 481*; R. Chiriquí Viejo Valley, on island near River, *White 150*; valley of the upper Río Chiriquí Viejo, 1300–1900 m., *White & White 12*.

This woodland species ranges from Jalisco to Peru. The Jalisco specimen (*Mexia 1899*) is atypical in having a circumscissile capsule, in that respect resembling the Galapagos species *P. darwinii* Hook. f. Standley (in Jour. Wash. Acad. 13:368. 1923.) describes *P. calospermum* from Salvador, and ascribes to it larger seeds, sepals and capsules than occur in *P. sprucei*. The larger seed size is not always correlated with the larger sepals. Variations in sepal and capsule size are frequently great enough in single specimens to embrace the descriptions of both species, so they are here concluded to be conspecific.

2. PLEUROPETALUM PLEIOGYNUM (O. Ktze.) Standl. in Jour. Wash. Acad. 13: 369. 1923.

Celosia pleiogyna O. Ktze. Rev. Gen. 541. 1891.
Pleuropetalum standleyi Suessenguth, in Rep. Spec. Nov. 44:41. 1938.

Erect sparingly branched subglabrous suffruticose herbs or shrubs to 3 m. high. Leaves glabrous to minutely strigillose on the veins below, lanceolate to rhombic-ovate, often falcate, apically attenuate, basally acute to subrounded, 3–15 cm. long, 1–5 cm. broad; petioles 5–25 mm. long. Inflorescences of mostly terminal racemes or panicles, the rhachises usually glandular. Flowers perfect, on pedicels 1–5 mm. long; bracts and bracteoles subequal, broadly ovate, carinate, 0.5–2 mm. long; sepals 5 (–6), subequal, ovate, concave, glabrate or scurfy, rounded to acute, with 19–27 ribs, 2.5–6 mm. long, 1–4 mm. broad; stamens 6–8; filaments 2–3 mm. long; filament tube 1–2 mm. long; anthers oblong; ovary globose to ellipsoid; styles 1, sulcate, about 0.5 mm. long; stigmata 5–6, rarely more or less, usually longer than the style, ultimately reflexed. Fruit a circumscissile capsule equaling or exceeding the sepals, red becoming black, 5–7 mm. long, 4–7 mm. broad; seeds cochleate-orbiculate, black, lustrous, reticulate, 1–1.2 (–1.5) mm. broad, on filiform or flattened funicles becoming 1–3 mm. long.

CANAL ZONE: vicinity of Las Cruces, 26–40 m., *Seibert 578*; drowned forest of Quebrada Culebra, *Dodge & Allen 17051*; forests along the banks of Quebrada Fea, Q. Pura and Cañon of R. Chagres, *Dodge & Allen 17405*; drowned forest of Quebrada Bonita and along its branches, 70–80 m., *Steyermark & Allen s. n.*; drowned forest of Quebrada Ancha, 70 m., *Steyermark & Allen s. n.* CHIRIQUÍ: Galera Chorcha, vicinity of Gualaca, alt. 1000 ft., *Allen 5054*. DARIÉN: Río Sabana, *Leopold 196*; Cana and vicinity, *Williams 727*. PANAMÁ: Cerro Campana, alt. 800 m., *Allen 4024*.

This species is apparently confined to Costa Rica, the type locality, and Panama. It occurs in rather deep woods, especially along streams in ravines and drowned forests.

2. CELOSIA L.

Celosia L. Sp. Pl. 205. 1753.

Amaranthus Adans. Fam. Pl. 2:269. 1763. not L. 1753.
Sukana Adans. loc. cit. 269. 1763.
Lestibudesia Thouars, Hist. Vég. Illes Afr. 53. 1806.
Lophoxera Raf. Fl. Tell. 3:42. 1837.
Gonufas Raf. Sylva Tell. 124. 1838.

Flowers perfect, the uppermost occasionally sterile, subsessile or short pedicellate, unibracteate and bibracteolate. Sepals 5, discrete, hypogynous, concave, variously colored, not strongly ribbed. Petals absent. Stamens 5, hypogynous, connate less than half their length forming an appendiculate or exappendiculate tube shorter than the ovary; filaments flattened; anthers 4-locellate, introrse, medially attached. Ovary subglobose to ellipsoid, 1-locular, multi-ovulate; ovules campylotropous; funicles flattened, exarillate, with free central placentation; styles 1; stigmata 2–3. Fruit a 2- to many-seeded circumscissile capsule; seeds cochleate-orbiculate, dark reddish brown to black, reticulate. Glabrate or pubescent herbaceous of suffruticose perennials or annuals. Leaves alternate, entire, subsessile to petiolate, glabrous or pubescent, lanceolate to rhombic-elliptic, deciduous. Inflorescences of terminal and axillary panicles or spikes, with or without foliar leaves.

A large genus of some fifty species, this seems to have reached its best development in subtropical regions of America, Africa and Asia. Only one species, the cultivated cockscomb, is so far reported from Panama.

Fig. 112. *Celosia argentea*

1. Celosia argentea L. Sp. Pl. 205. 1753.

Celosia cristata L. loc. cit. 205. 1753.
Celosia margaritacea L. Sp. Pl. ed. 2:297. 1763.
Celosia coccinea L. loc. cit. 297. 1763.
Celosia pyramidalis Burm. Fl. Ind. 65. 1768.
Celosia marilandica Retz. Obs. Bot. 3:27. 1783.
Celosia pallida Salisb. Prodr. 145. 1796.
Celosia huttonii Mast. in Gard. Chron. 215. 1872.
Amaranthus purpureus Nieuwl. in Amer. Midl. Nat. 3:279. 1914.

Erect glabrous simple or much branched annuals to 1 m. high. Leaves glabrous, linear-lanceolate to rhombic or ovate, apically acuminate to acute, 3–12 cm. long, 0.5–6 cm. broad; petioles 1–30 mm. long. Inflorescence of simple (quite complex, often fasciated, in cultivated varieties) pedunculate cylindric spikes 2–20 cm. long, 1–2 cm. broad. Flowers perfect, the uppermost occasionally sterile, sessile; bracts and bracteoles subequal, ovate, mucronate, 2–7 mm. long; sepals 5, subequal, ovate, concave, mucronate, white to pinkish (variously colored in cultivated varieties), erect in fruit, 6–10 mm. long; stamens 5, 3–5 mm. long, the tube shorter than the free portions of the filaments; pseudostaminodia minute and deltoid or absent; anthers oblong; ovary ellipsoid; style 1, 3–6 mm. long, usually exceeding the sepals; stigmata 2 (–3), minute. Fruit a circumscissile capsule, shorter than the calyx, 3–4 mm. long; seeds (1–) 3–6 (–9), cochleate-orbiculate, dark reddish brown, about 1.5 mm. broad.

Cultivated in many regions, possibly natives of Africa, the cockscombs are reported by Standley (in Contr. U. S. Nat. Herb. 27:172. 1928) to be cultivated in gardens in Panama, where they are called *abanico*. The cultivants often escape and morphologically approach the natural variety. Backer (in Fl. Mal. 4^2:74. 1949.) notes that in some escapes, one branch may bear the mark of cultivation with another resembling the wild form. He informs us that the seeds are used by the Chinese for poultices and for adorning cakes, while the leaves furnish an inferior vegetable. In India, where it is used medicinally and as a vegetable, it often appears spontaneously in paddy and ragi fields. Among vernacular names reported from Mexico and Central America are *moño, san josé, cresta de gallo, amor seco, mano de león, flor de mano, amaranto* and *boria*.

3. AMARANTHUS L.

Amaranthus L. Sp. Pl. 989. 1753.

Bliton Adans. Fam. Pl. 2:506. 1763.
Bajan Adans. loc. cit. 506. 1763.
Roemeria Moench, Meth. 341. 1794.
Glomeraria Cav. Descr. 319. 1803.
Dimeiandra Raf. Neogen. 2. 1825.
Scleropus Schrad. Ind. Sem. Hort. Gott. 1835.; in Linnaea 11: Litt.-ber. 89. 1837.
Dimeianthus Raf. Fl. Tell. 3:41. 1837.
Amblogyna Raf. loc. cit. 42. 1837.
Euxolus Raf. loc. cit. 42. 1837.
Pentrius Raf. loc. cit. 42. 1837.

Albersia Kunth, Fl. Berol. ed. 2. 144. 1838.
Mengea Schauer, in Meyer, Nov. Acta Acad. Leop. 19: Supply. 1:405. 1843.
Pyxidium Moq. in DC. Prodr. 13^2:262. 1849.
Sarratia Moq. loc. cit. 262. 1849.
Galliaria Bubani, Fl. Pyren. 1:184. 1897.

Flowers monoecious, dioecious or polygamous, sessile or subsessile, unibracteate and bibracteolate. Sepals 3–5, rarely 1, discrete, hypogynous, concave, occasionally basally clawed, equal or subequal, membranaceous, erect and persistent in fruit. Stamens 3–5, rarely 1, hypogynous, discrete; filaments filiform; anthers 4-locellate, introrse, medially attached, oblong. Ovary ovoid to lenticular, 1-locular, 1-ovulate, the ovule campylotropous on a short exarillate funicle, the placentation basal; styles 1–3; stigmata 2–3, usually exceeding the styles. Fruit a utricle, indehiscent or circumscissile; seeds cochleate-orbiculate, smooth to minutely verrucose. Leaves alternate, entire to minutely crenulate, long-petiolate. Erect or prostrate, glabrous to pubescent annual herbs. Inflorescences of terminal and/or axillary spicate or paniculate thyrses, in Panama monoecious or polygamous with female flowers basally, hermaphroditic flowers medially, and male flowers distally, the latter tending to have longer, narrower sepals.

Widespread in both temperate and tropical regions throughout the world, *Amaranthus* consists of perhaps fifty species. Many of them are inhabitants of open disturbed areas where they may become rather annoying weeds. Some are cultivated for their edible seeds and leaves, and others, with brightly colored inflorescences, are planted as ornamentals. Sauer (Ann. Missouri Bot. Gard. 37: 561–632. 1950) reports on the detailed ethnological history of the grain-amaranths. Seven species have been reported in Panama, but one, adventive on San Jose Island, apparently no longer persists.

a. Stamens and sepals 1–3, the sepals mostly less than 1.5 mm. long; utricle rugulose.
  b. Inflorescences terminal and axillary; sepals of the pistillate flowers 3, the bracts about equaling them in length; stamens 3 ..... 1. A. VIRIDIS
  bb. Inflorescences all axillary; sepals of the pistillate flowers mostly 1–2, about half as long as the bracts; stamens mostly 2 ..... 2. A. CALIFORNICUS
aa. Stamens and sepals 5, the sepals mostly more than 1.5 mm. long; utricle smooth or rugulose.
  c. Utricle subglobose; stylopodium circular in cross section; sepals red or purple; plants unarmed ..... 3. A. CRUENTUS
  cc. Utricle compressed-ovoid; stylopodium 2–3-lobulate in cross section; sepals greenish; plants armed or unarmed.
    d. Plants unarmed; axillary inflorescences cylindric.
      e. Thyrses less than 6 mm. broad; bracts of the pistillate flowers mostly shorter than the sepals, some of the sepals spatulate ..... 4. A. DUBIUS
      ee. Thyrses more than 6 mm. broad; bracts of the pistillate flowers mostly longer than the sepals, giving the spikes a bristly appearance; none of the bracts spatulate ..... 5. A. HYBRIDUS
    dd. Plants armed; axillary inflorescences globose ..... 6. A. SPINOSUS

In addition to the aforementioned, Johnston (in Sargentia 8:124. 1949) adds that *A. retroflexus* L. was collected on San Jose Island in 1945 (*Erlanson 188*), but was unsuccessfully searched for in 1946. I have not seen the specimen. The

species is separated from the closely allied species *A. hybridus* by the obtuse sepals of the pistillate flowers.

1. Amaranthus viridis L. Sp. Pl. 2:1405. 1763.

Chenopodium caudatum Jacq. Coll. 2:325. 1788.
Amaranthus gracilis Desf. Tabl. Bot. 43. 1804.
Albersia gracilis Webb. & Berth. Phyt. Canar. 3:287. 1836.
Euxolus caudatus Moq. in DC. Prodr. 13^2:274. 1849.
Euxolus caudatus β gracilis Moq. loc. cit. 13^2:274. 1849.
Euxolus caudatus γ maximus Moq. loc. cit. 13^2:274. 1849.

Rather delicate glabrous annuals to as much as 1 m. high, the branches ascending. Leaves glabrous; entire to minutely crenulate, deltoid- to rhombic-ovate, apically emarginate to rounded and mucronate, basally truncate to subacute, 1.5–6 cm. long, 1–4 cm. broad, the petioles 0.5–4 cm. long. Inflorescences of thyrses racemosely disposed, the terminal and axillary thyrses cylindric, mostly less than 7 mm. broad. Flowers polygamo-monoecious or monoecious; bracts and bracteoles subequal, lanceolate to ovate, ca. 1 mm. long; sepals 3, linear-oblong to obovate, rounded, mucronate, 1–1.5 mm. long, the midrib dark green, the margins scariose; stamens 3, discrete, 1–1.5 mm. long; ovary compressed-globose; style 1, minute, stigmata 3, longer than the style. Fruit an indehiscent, strongly rugose utricle, 1–1.5 mm. long, 1–1.5 broad; seeds cochleate-orbiculate, dark red to black, dull, minutely pebbled, 1–1.2 mm. broad.

Presumably a native of the Old World tropics, this weedy species is adventive around Balboa (fide Standley, in Contr. U. S. Nat. Herb. 27:173. 1928). It is also adventive in the eastern United States. The names *bledo* and *calalú* are applied to all the species of Panamanian *Amaranthus*, any of which may serve as potherbs.

2. Amaranthus californicus (Moq.) S. Wats. Bot. Calif. 2:42. 1880.

Mengea californica Moq. in DC. Prodr. 13^2:270. 1849.
Amaranthus carneus Greene, in Pittonia 2:105. 1890.
Amaranthus albomarginatus Uline & Bray, in Bot. Gaz. 19:318. 1894.

Prostrate, radially spreading delicate annuals, the branches to as much as 5 dm. long, often tinged with anthocyanins. Leaves glabrous, bullate, entire, often white-margined, ovate to obovate and spatulate, apically emarginate to rounded and mucronate, basally attenuate, 3–25 mm. long, 2–12 mm. broad, the petioles 3–25 mm. long. Flowers in axillary, often leafy, few-flowered clusters, with every node often bearing an inflorescence, these ultimately shorter than the petioles. Flowers monoecious; bracts and bracteoles lanceolate, apically aristate, 1.5–2.5 mm. long; sepals 3 and quite unequal, or 1–2 in the pistillate flowers, linear to lanceolate, acute to obtuse, 0.4–1.0 mm. long; sepals of the staminate flowers 3, subequal; stamens 2, discrete, ca. 1 mm. long; ovary ellipsoid, the stigmata 3, ca. as long as the ovary at anthesis. Fruit a utricle, circumscissile about the middle, rugose, 1–1.5 mm. long, 1–1.5 mm. broad; seeds cochleate-orbiculate, dark reddish-brown, lustrous, minutely pebbled, 0.8–1.1 mm. broad.

PANAMÁ: abandoned corral, San José Island, Perlas Archipelago, Gulf of Panama, ca. 55 mi. sse. of Balboa, *Johnston 1151*.

Although the cited specimen was labeled as *A. albus* L., the prostrate habit, few stamens, and reduced sepals in the pistillate flowers clearly separate it from that species. The small seeds and rugulose utricles also serve to separate it from *A. blitoides* S. Wats., a very closely related prostrate species.

3. AMARANTHUS CRUENTUS L. Syst. Veg. 10:1269. 1759.

Amaranthus paniculatus L. Sp. Pl. 2:1406. 1763.
Amaranthus flavus L. loc. cit. 2:1406. 1763.
Amaranthus sanguineus L. loc. cit. 1407. 1763.
Amaranthus parisiensis Schkuhr, Handb. 3:249. 1808.
Amaranthus speciosus Sims, Bot. Mag. *pl. 2227*. 1821.
Amaranthus paniculatus α *purpurascens* Moq. in DC. Prodr. 13^2:257. 1849.
Amaranthus paniculatus β *cruentus* Moq. loc. cit. 257. 1849.
Amaranthus hybridus paniculatus Uline & Bray, in Mem. Torr. Club 5:145. 1894.
Amaranthus dussii Sprenger, in Bull. Soc. Tosc. Ort. 3^1:178. 1896.
Galliaria patula Bubani, Fl. Pyren. 1:187. 1897.
Amaranthus hybridus subsp. *cruentus* Thellung, Fl. Adv. Montp. 205. 1912.

Coarse usually pubescent annuals to 2 m. high, simple or with ascending branches. Leaves glabrous above, pubescent or glabrate below, entire to minutely crenulate, ovate to rhombic, apically rounded to acute and mucronate, basally acute to cuneate, 3–15 cm. long, 1–6 cm. broad; petioles 1–8 cm. long. Inflorescences of thyrses racemosely disposed, the terminal and axillary thyrses cylindric, often drooping, 5–15 mm. broad. Flowers polygamo-monoecious or monoecious; bracts and bracteoles subequal, lanceolate to ovate, 1.5–2.5 mm. long; sepals 5, oblong to ovate, rounded to mucronate apically, 1.5–2 mm. long, the midribs dark green, the margins scariose and tinted with anthocyanins; stamens 5, discrete, 1–2 mm. long; ovary compressed globose, capped by a circular stylopodium; stigmata 3 (–4), longer than the stylopodium. Fruit a smooth to rugulose subglobose utricle, circumscissile near the middle, about 2 mm. long, usually exceeding the sepals; seeds cochleate-orbiculate, dark reddish brown to black, minutely reticulate, 1–1.3 mm. broad.

This is the commonly cultivated grain amaranth of Central America. In Panama it is called *abanico chino* and *calalú*, and it is cultivated both as an ornamental and as a potherb. In Mexico and Guatemala the seeds are used in making sweetbreads and mushes. Standley & Steyermark (in Field Mus. Bot. 24^4:153. 1946) point out that *A. caudatus* L., *A. leucosperma* Wats. and *A. cruentus* L. are best treated as one species "rather doubtfully distinct from *A. hybridus*." Sauer (Ann. Missouri Bot. Gard. 37:561–632. 1950) on the other hand contends that there are four major grain amaranth species in the Americas, *A. leucocarpus* Wats., chiefly in Mexico; *A. cruentus* L., chiefly in Guatemala; *A. caudatus* L., chiefly in the Andes; and *A. edulis* Spegazzini, chiefly in Argentina. Of the cultivated amaranths, whether they comprise several or one species, he cites only *A. cruentus* from Panama.

4. Amaranthus dubius Mart. Pl. Hort. Erlang. 197. 1814.

Amaranthus tristis Willd. Hist. Amaranth. 21. 1790. not *A. tristis* L.
Amaranthus incomptus Willd. Enum. Hort. Berol. suppl.: 64. 1813. hyponymn.
Amaranthus tristis β xanthostachys Moq. in DC. Prodr. 13^2:260. 1849.
Amaranthus tristis γ flexuosus Moq. loc. cit. 260. 1849.
Amaranthus tristis δ leptostachys Moq. loc. cit. 260. 1849.
Amaranthus dubius B *xanthostachys* Thellung, in Asch. & Graebn. Syn. Mittel-Eur. Fl. 5: 266. 1914.
Amaranthus dubius C *flexuosus* Thellung, loc. cit. 266. 1914.
Amaranthus dubius D *leptostachys* Thellung, loc. cit. 266. 1914.

Rather delicate mostly glabrous annuals to 1 m. high with ascending branches. Leaves glabrous or glabrate, entire or minutely crenulate, deltoid- to rhombic-ovate, apically rounded to acute, often mucronate, basally rounded to acute, 2–8 cm. long, 1–6 cm. broad; petioles 1–6 cm. long. Inflorescences of thyrses racemosely disposed, the terminal and axillary thyrses mostly cylindric and less than 6 mm. broad. Flowers polygamo-monoecious or monoecious; bracts and bracteoles subequal, lanceolate to ovate or obovate, acute to acuminate, 1.5–2 mm. long, the midribs dark green, the margins scariose; stamens discrete, 1–3 mm. long; ovary ovoid; styles (2–) 3, fimbrillate. Fruit a slightly rugose compressed ovoid utricle, circumscissile about the middle, 1.5–2.5 mm. long; seeds cochleate-orbiculate, reddish brown to black, reticulate, 0.8–1.1 mm. broad.

Bocas del Toro: Isla Colón, vicinity of Chiriquí Lagoon, *von Wedel 2854*. Canal Zone: near Gorgas Memorial Laboratory, vicinity of Miraflores, *G. White 119*; in government forest along Las Cruces Trail, *Hunter & Allen 712*; Bohio Soldado, *Cowell 235*. Darién: vicinity of Boca de Cupe, ca. 40 m., *Allen 874*. Panamá: Agricultural Exp. Sta. at Matías Hernández, *Pittier 6859*.

Reputedly the common weed amaranth of the Caribbean, this species extends from Mexico through tropical South America and is adventive in Europe. In Panama, where the leaves and young shoots are employed as potherbs, the names *bledo* and *calalú* are applied. The Mayas call it *xetz* and *chactez*; Mexicans call the amaranths *quelite*, a name derived from an Aztec word and used for any potherb. The specific epithet is strongly suggestive of its specific status. It is weakly separated from *A. hybridus* L., from which it is frequently keyed by the length of the sepals in proportion to the length of the utricles. In individuals of both species, however, the utricles vary from shorter to longer than the sepals.

5. Amaranthus hybridus L. Sp. Pl. 990. 1753.

Amaranthus hypocondriacus L. Sp. Pl. 991. 1753.
Amaranthus hecticus Willd. Hist. Amaranth. 25. 1790.
Amaranthus strictus Willd. loc. cit. 27. 1790.
Amaranthus laetus Willd. loc. cit. 28. 1790.
Amaranthus chlorostachys Willd. loc. cit. 34. 1790.
Amaranthus retroflexus var. *hybridus* A. Gray, Man. ed. 5:412. 1867.
Amaranthus retroflexus var. *chlorostachys* A. Gray, loc. cit. 412. 1867.
Amaranthus chlorostachys var. *hybridus* S. Wats. in A. Gray, Man. ed. 6:428. 1889.
Amaranthus hybridus var. *hypocondriacus* B. L. Robinson, in Rhodora 10:32. 1908.
Amaranthus hybridus 2 *chlorostachys* G. Beck, in Reichenb. Ic. Fl. Germ. 24:175. 1908.
Galliaria hybrida Nieuwl. in Am. Midl. Nat. 3:278. 1914.

Fig. 113. *Amaranthus dubius*

Rather coarse often pubescent annuals to 2.5 m. high with ascending branches. Leaves pubescent or glabrous, entire to minutely crenulate, deltoid- to rhombic-ovate, apically rounded to acute, often mucronate, basally acute to rounded, 2–15 cm. long, 1–7 cm. broad; petioles 1–8 cm. long. Inflorescences of congested thyrses racemosely disposed, the terminal and axillary thyrses mostly cylindric, 6–12 mm. broad. Flowers polygamo-monoecious or monoecious; bracts and bracteoles subequal, lanceolate to ovate, 2–4 mm. long, often conspicuously longer than the flowers; sepals lanceolate to ovate or obovate, acute to acuminate, 1.5–2.5 mm. long, the midribs dark green, the margins scariose, rarely tinged with anthocyanins; stamens 5, discrete, 1–3 mm. long; ovary ovoid; styles (2–) 3, conical; stigmata (2–) 3, fimbrillate. Fruit a slightly rugose compressed ovoid utricle, circumscissile near the middle, 2–2.5 mm. long; seeds cochleate-orbiculate, reddish brown to black, minutely reticulate, 1–1.3 mm. broad.

CHIRIQUÍ: vicinity of Boquete, 1200–1500 m., *Woodson & Schery 722*.

This weedy species, frequently forming large stands in old fields, is found throughout temperate and tropical North and South America, and is adventive in many parts of the Old World. Vernacular names reported in Mexico and Central America are *quintoniles, calete, ses, huisquilete* and *quiec tes, bledo, xtez, quelite* and *huisquelite*. The leaves and young shoots are often cooked as potherbs.

6. Amaranthus spinosus L. Sp. Pl. 991. 1753.

Amaranthus diacanthus Raf. Fl. Ludov. 31. 1817.
Amaranthus caracasanus H.B.K. Nov. Gen. & Sp. 2:195. 1817.
Amaranthus spinosus α rubricaulis Hassk. Flora 25: litt. 20. 1842.
Amaranthus spinosus β viridicaulis Hassk. loc. cit. litt. 20. 1842.
Amaranthus spinosus ζ pygmaeus Hassk. Cat. Pl. Bogor. 83. 1844.
Amaranthus spinosus β purpurascens Moq. in DC. Prodr. 13^2:260. 1849.
Amaranthus spinosus f. *inermis* Schum. & Laut. Fl. Deuts. Schutzg. Südsee 305. 1900.
Amaranthus spinosus I circumscissus Thellung in Asch. & Graebn. Syn. Mittel-Eur. Fl. 5: 269. 1914.
Amaranthus spinosus II basiscissus Thellung, loc. cit. 269. 1914.
Amaranthus spinosus III *indehiscens* Thellung, loc. cit. 269. 1914.
Galliaria spinosa Nieuwl. in Am. Midl. Nat. 3:278. 1914.

Rather coarse, mostly glabrous armed annuals to 2 m. high, usually with erect branches. Leaves glabrous or pubescent below, narrowly rhombic-ovate, apically rounded to acute, basally acute to cuneate, 1–12 cm. long, 0.5–5 cm. broad; petioles 0.5–8 cm. long, with 2 thorns in their axils. Inflorescences of terminal and axillary thyrses racemosely disposed, the lower axillary thyrses globose and up to 15 mm. broad. Flowers polygamo-monoecious or monoecious, the bracts and bracteoles rather variable, lanceolate to acicular, 1–5 mm. long, often resembling the thorns, some conspicuously longer than the flowers; sepals 5, lanceolate to oblong, 1–2.5 mm. long, the midribs dark-green, the margins scariose; stamens discrete, 1–2 mm. long; ovary ovoid; styles 3, conical; stigmata 3, fimbrillate. Fruit a slightly rugose compressed ovoid utricle, irregularly to regularly circumscissile, 1.5–2.5 mm. long; seeds cochleate-orbiculate, reddish brown to black, minutely reticulate, 0.7–1.0 mm. broad.

CANAL ZONE: Monkey Hill and vicinity, *Cowell 19*. CHIRIQUÍ: vicinity of Boquete, 1200–1500 m., *Woodson & Schery 723*; vicinity of Puerto Armuelles, 0–75 m., *Woodson & Schery 833*. COLÓN: Culebra, *Cowell 214*. HERRERA: vicinity of Ocu, 100 m., *Allen 4086*.

Presumably a native of America, this anthropochorous species now has a circumpolar distribution in temperate and tropical countries. In Panama it is probably called *bledo* and *calalú*. Other Mexican and Central American names are *xtez, kix-xtez, huisquelite, bledo macho, ixtez, tsetz, labtzetz* and *nigua*. In spite of the rather formidable thorns this species is also utilized as a potherb.

4. CHAMISSOA HBK.

CHAMISSOA HBK. Nov. Gen. & Sp. 2:196. 1817.

Kokera Adans. Fam. Pl. 2:269. 1763. hyponym.

Flowers perfect, subsessile, with 1–3 bracts subtending 1–5 bracteate fertile and 0–4 bracteate sterile flowers. Sepals 5, discrete, hypogynous, concave, greenish white, with conspicuous midribs and membranaceous margins. Stamens 5, hypogynous or perigynous, basally connate forming an exappendiculate tube shorter than, but occasionally basally fused with, the ovary; free portions of the filaments longer than the tube, usually somewhat flattened; anthers 4-locellate, introrse, medially attached. Ovary globose or ovoid, 1-locular, 1-ovulate; ovules campylotropous, the filiform arillate funicles with central basal placentae; styles 1, stigmata 2 (–3). Fruit a utricle circumscissile near the middle; seeds cochleate-orbiculate, black. Erect or clambering glabrate or pubescent herbs or shrubs. Leaves alternate, entire, petiolate or subsessile, linear-elliptic to broadly ovate, attenuate, deciduous. Inflorescences of axillary and terminal glomerules, these racemosely or paniculately disposed, with or without foliar leaves.

This genus of perhaps five species, is chiefly a South and Central American genus with only one species ranging as far north as Mexico. The closely related oriental genus *Allmania* has occasionally been treated as a subgenus but morphologically seems to deserve generic status. Two species of *Chamissoa* occur in Panama.

a. Terminal inflorescences pyramidal, the glomerules paniculately disposed; styles less than 1.5 times as long as the stigmata; ovary at anthesis tympaniform, truncate to the base of the style; sepals ovate, the outer more than 1 mm. broad; aril completely enveloping the seeds; seeds punctate..... 1. C. ALTISSIMA

aa. Terminal inflorescences cylindric, the glomerules racemosely disposed; styles 2 times as long as the stigmata; ovary at anthesis doleiform, attenuate to the base of the style; sepals lanceolate, the outer less than 1 mm. broad; aril minute; seeds verrucose..... 2. C. MAXIMILIANA

1. CHAMISSOA ALTISSIMA (Jacq.) HBK. Nov. Gen. & Sp. 2:197. 1817.

Celosia paniculata L. Sp. Pl. ed. 2:298. 1762. not L. 1753.
Achyranthes altissima Jacq. Enum. Pl. Carib. 17. 1762
Chamissoa macrocarpa HBK. Nov. Gen. & Sp. 2:197. 1817.

Fig. 114. *Chamissoa altissima*

Celosia tomentosa Willd. in Roem. & Schult. Syst. Veg. 5:531. 1819.
Achyranthes linkiana Roem & Schult. Syst. Veg. 5:545. 1819.
Chamissoa martii Moq. in DC. Prodr. 13²:252. 1849.
Chamissoa altissima β *laxiflora* Moq. loc. cit. 251. 1849.
Chamissoa altissima γ *densiflora* Moq. loc. cit. 251. 1849.
Chamissoa altissima var. β *glabrata* Seub. in Mart. Fl. Bras. 5¹:242. 1875
Kokera paniculata O. Ktze. Rev. Gen. 542. 1891.
Chamissoa altissima var. *rubella* Suesseng. in Rep. Spec. Nov. 35:306. 1934.
Chamissoa altissima subsp. *albo-grisea* Suesseng. in Rep. Sp. Nov. 39:6. 1935.
Chamissoa altissima var. *grandispicata* Suesseng. loc. cit. 6. 1935.
Chamissoa altissima var. *grandispicata* f. *semispicata* Suesseng. loc. cit. 6. 1935.
Chamissoa altissima var. *densi-paniculata* Suesseng. in Lilloa 4:129. 1939.

Clambering subglabrous shrubs or vines to 3 m. high. Leaves glabrous or slightly pilose, broadly lanceolate to ovate, apically acute to acuminate and mucronate, basally truncate to acute, 3–14 cm. long, 1–6 cm. broad; petioles 0.5–3.5 cm. long. Inflorescences of glomerules paniculately disposed, the pubescent primary rhachis usually visible at intervals. Flowers perfect, some usually sterile, subsessile; bracts 1–3, broadly deltoid, carinate, mucronate, with membranaceous margins, 1–1.5 mm. long, 1–1.5 mm. broad; sepals 5, subequal, ovate, concave, acute to mucronate, 5-nerved, greenish white, 2.5–4 mm. long, 1–1.5 mm. broad; stamens 5; filaments 1.5–3 mm. long; filament tube 0.5–1 mm. long, often basally adnate to the ovary; anthers globose to oblong; ovary at anthesis tympaniform to globose, usually as broad as long and truncate or flanged at the summit; style 1, 0.5–1 mm. long, usually shorter than the stigmata; stigmata 2 (–3), erect at anthesis, reflexed in fruit. Fruit a utricle, exserted, circumscissile near the middle, compressed ovoid, the summit conspicuously operculate and truncate to inconspicuously operculate and rounded, 3–5 mm. long, 2–3.5 mm. broad, aril bivalvate, becoming wrinkled, brownish white, completely investing the seeds; seeds smooth but punctate, black, lustrous, 2–2.5 mm. broad.

BOCAS DEL TORO: Changuinola Valley, *Dunlop 309*; vicinity of Chiriquí Lagoon, *von Wedel 1380 & 1799*; Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 634A, 840 & 1641*; Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 1896 & 2141*; Garay Creek, vicinity of Chiriquí Lagoon, *von Wedel 2637*. CANAL ZONE: between Summit and Gamboa, *Greenman & Greenman 5258*. COCLÉ: vicinity of El Valle, 600–1000 m., *Allen 1205*; El Valle de Antón, trail near Finca Tomás Arias, 600 m., *Allen 4230*. DARIÉN: Tucutí, Chepigana, *Terry & Terry 1382*. PANAMÁ: Taboga Island, on more or less forested slopes, *MacBride 2823*.

This most commonly collected species in the genus ranges from Mexico to Argentina, usually in thickets where it tends to clamber over adjacent plants. Of limited occurrence in amazonian South America is a rather distinct type often regarded as a separate species, *C. macrocarpa* HBK., with rounded exoperculate, frequently 3-stylate utricles much longer than the sepals. Kuntze (Rev. Gen. 542. 1891), perhaps the first lumper, regards *C. macrocarpa* as conspecific with *C. altissima*. Annotation labels reveal that Schinz at one time considered *C. macrocarpa* as only a variety of *C. altissima*, and finally Suessenguth (in Rep. Sp. Nov. 35:306. 1934) admits that a sharp distinction between the two is impossible.

2. Chamissoa maximiliana Mart. ex Moq. in DC. Prodr. 13²:251. 1849.

Chamissoa celosioides Griseb. in Goett. Abh. 19:79. 1874.
Chamissoa maximiliana var. *β procumbens* Seub. in Mart. Fl. Bras. 5¹:243. 1875.
Kokera celosioides (Griseb.) O. Ktze. Rev. Gen. 543. 1891.
Kokera acuminata (Mart.) O. Ktze. loc. cit. 543. 1891.
Chamissoa maximiliana var. *pubescens* Chod. in Bull. Herb. Boiss. 7:63. 1899.
Chamissoa maximiliana f. *celosioides* (Griseb.) Suesseng. in Rep. Sp. Nov. 35:306. 1934.

Clambering subglabrous herbs, shrubs or vines to 2 m. high. Leaves glabrous or slightly pilose, narrowly to broadly ovate, apically acuminate to mucronate, basally acute to rounded, 2.5–10 cm. long, 1–4 cm. broad; petioles 1–2.5 cm. long. Inflorescences of glomerules racemosely disposed, the pubescent primary rhachis usually obscured. (In the typical form the glomerules are not all closely approximated and the rhachis is visible at intervals.) Flowers perfect, some usually sterile, or tending to monoecism, subsessile; bracts 1–3, narrowly deltoid to lanceolate, carinate, mucronate, with membranaceous margins, 1.5–2 mm. long, 1–1.5 mm. broad; sepals 5, subequal, lance-oblong, concave, acuminate to mucronate, obscurely 3–7 nerved, greenish white, 3–4 mm. long, 0.5–1 mm. broad; stamens 5; filaments 1.5–3 mm. long; filament tube about 0.5 mm. long; ovary at anthesis doleiform, 1–2 times as long as broad, attenuate to the base of the style, often lobulate or flanged near the summit; style 1, 1–1.5 mm. long, longer than the stigmata; stigmata 2, erect at anthesis, reflexed in fruit. Fruit a utricle, usually included, circumscissile near the middle, globose to ovoid, the summit operculate and usually truncate, 2–3.5 mm. long, about 2 mm. broad; aril minute; seeds verrucose, black, often pleiochroistic, 1.5–2 mm. broad.

Bocas del Toro: Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 1441*; vicinity of Chiriquí Lagoon, *von Wedel 1695*. Darién: vicinity of Cana, 1750 ft., *Stern, Chambers et al. 677*.

Inhabiting thickets and forest clearings, this species ranges from Costa Rica to Argentina. The Panama specimens seem referable to the forma *celosioides* (Griseb.) Suesseng. which differs from the typical form in possessing compact inflorescences. The type of *C. maximiliana* has lax inflorescences with subglobose operculate utricles. Three other species with minute arils occur in South America. *C. acuminata* Mart., with smooth seeds and petiolate, narrowly ovate falcate leaves, occurs in Brazil and northern Argentina. *C. blanchetii* Moq., with smooth but punctate seeds and subsessile linear-elliptic leaves, occurs in Brazil. *C. brasiliana* (Moq.) R. E. Fr., native to Brazil and Argentina, differs from all other species in having axillary verticillate glomerules.

5. ACHYRANTHES L.

Achyranthes L. Sp. Pl. 20. 1753.

Centrostachys Wall. in Roxb. Fl. Ind. 2:497. 1824.
Cadelaria Raf. Fl. Tell. 3:39. 1837.
Stachyarpagophora Vaill. in Maza, Fl. Haban. 92. 1897.

Flowers perfect, bracteate and bibracteolate, subsessile in elongate spikes.

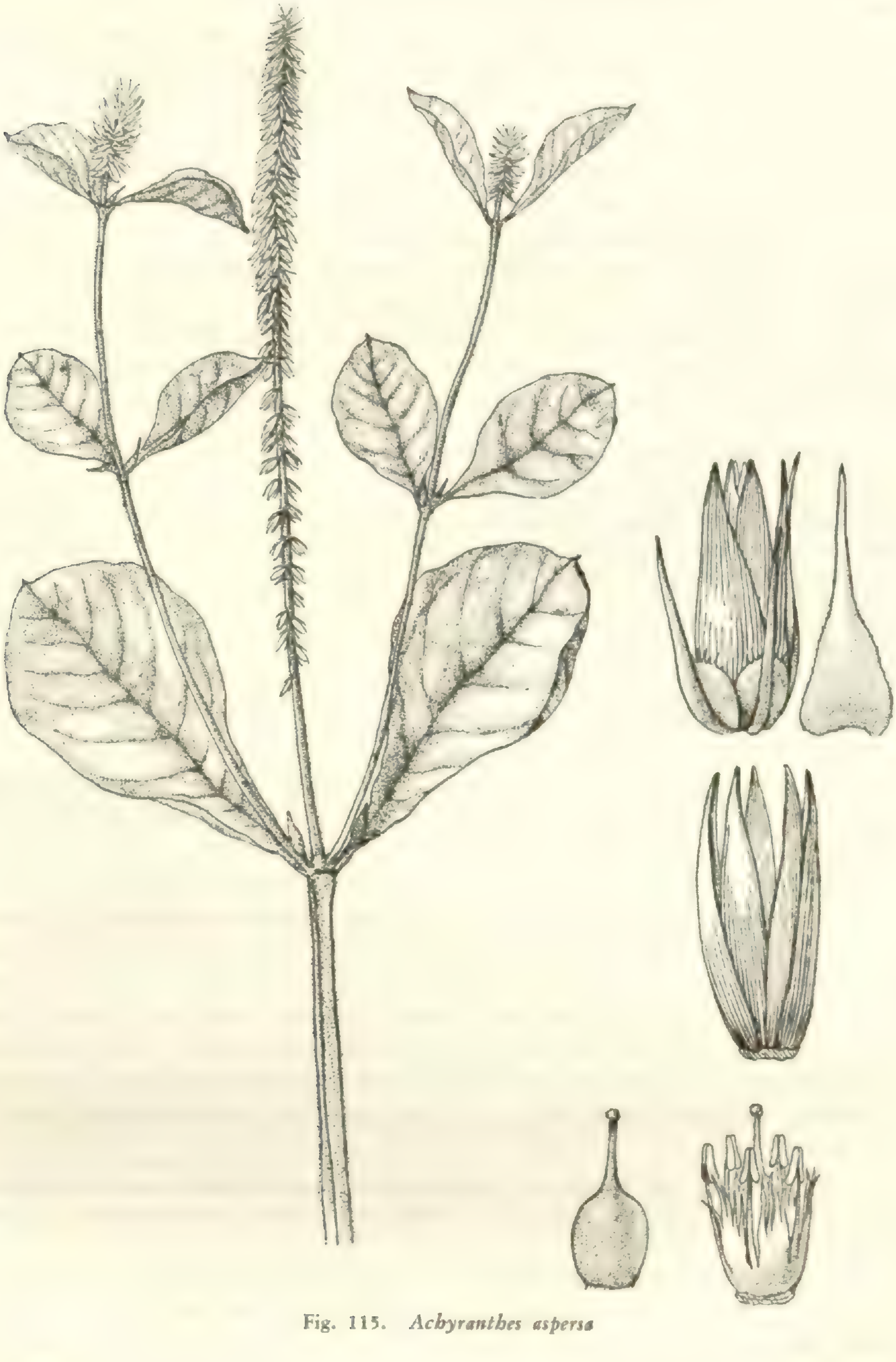

Fig. 115. *Achyranthes aspersa*

Sepals 4–5, discrete, hypogynous, concave, subequal, obscurely 3–5 nerved, occasionally pungent. Stamens 2–5, the filaments flattened and united below forming an appendiculate tube; anthers 4-locellate, introrse, medially attached. Ovary obovoid, 1-locular, 1-ovulate; ovules campylotropous on elongate flattened funicles; style 1, filiform; stigma 1, capitate. Fruit a membranaceous turbinate indehiscent utricle; seeds cochleate-orbiculate, reddish brown. Glabrous to pubescent erect or decumbent annual or perennial herbs. Leaves opposite, short-petiolate, scantily appressed strigose to sericeous, deciduous. Inflorescences of terminal and axillary spikes, the flowers deflexed in age, the spinose tips of the bracts not uncinate.

This weedy genus, of about five species, mostly of the Old World, is represented by one species in Central America. The spines of the inflorescences are often a source of discomfort. Two varieties of one species occur in Panama.

1. ACHYRANTHES ASPERSA L. Sp. Pl. 204. 1753.

Achyranthes aspersa β indica L. loc. cit. 204. 1753.
Achyranthes indica Mill. Gar. Dict. ed. 8: no. 2. 1768.
Achyranthes argentea Lam. Encycl. 1:545. 1785.
Achyranthes obtusifolia Lam. loc. cit. 545. 1785.
Achyranthes sicula Roth, Cat. Bot. 1:39. 1797.
Cadelaria sicula Raf. Fl. Tell. 3:39. 1837.
Cadelaria indica Raf. loc. cit. 39. 1837.
Stachyarpagophora aspersa Maza, Fl. Haban. 93. 1897.
Achyranthes aspersa simplex Millsp. in Field. Mus. Bot. 2:36. 1900.
Centrostachys indica (L.) Standl. in Jour. Wash. Acad. 5:75. 1915.
Centrostachys aspersa (L.) Standl. loc. cit. 75. 1915.

Erect or procumbent pubescent annuals or perennials, the usually branched stems to 2 m. long. Leaves scantily to densely pubescent, ovate to orbicular, apically acuminate to rounded, basally cuneate to rounded, 2–25 cm. long, 2–9 cm. broad; petioles 2–25 mm. long. Inflorescences of terminal and axillary pedunculate spikes, 3–40 cm. long, 6–12 mm. broad, the flowers deflexed. Flowers perfect; bracts and bracteoles subequal, 2–3.5 mm. long, ovate, spinescent, the tips rarely arcuate but not uncinate; sepals 4–5, greenish white, subequal, hypogynous, obscurely nerved, 4–7 mm. long; stamens 5, united below into a short tube; pseudostaminodia lacerate, exceeded by the 4-locellate anthers; ovary obovoid; style 1, filiform, at anthesis longer than the ovary; stigma 1, capitate. Fruit an indehiscent turbinate utricle; seeds cochleate-orbiculate, reddish brown, about 1 mm. broad.

BOCAS DEL TORO: *H. Wedel 418.* CANAL ZONE: Gatún, *Cowell 300*; near Frijoles, *Pittier 6834*; around Culebra, 50–150 m., *Pittier 4068.* PROVINCE UNKNOWN: *Sutton Hayes 320.*

A rather ubiquitous pantropical weed, this species is perhaps adventive in America. In India the dried inflorescences are used by orthodox Hindus in sacred pyres. Standley & Steyermark (in Field Mus. Bot. 24^4:145. 1946), who maintain *A. indica* as specifically distinct from *A. aspersa*, say that *A. indica* is scarce in Central America and known only from the Atlantic Coast, in contrast to the

widely distributed *A. aspersa*. The variety *indica* seems to be rather regularly distinct from the variety *aspersa* in having rounded leaves and shorter sepals. All the cited specimens except *Hayes 320* seem referable to the variety *indica*. Many vernacular names are reported; *zacpaiché* and *zorillo blanco* in the Yucatan, *abrojo* in Salvador, *mozote* in Salvador and Honduras, *mozotillo* and *rabo de chanco* in Costa Rica, *cola de armado, penegato, pije de gato* and *chile de perro* in Guatemala where the typical variety is apparently distinguished by the natives from the variety *indica* to which the names *pegapega, goincilla* and *mozotlexc* are applied.

6. CYATHULA Lour.

CYATHULA Lour. Fl. Cochinch. 1:101. 1790.

Polyscalis Wall. Cat. no. 6939. 1832.

Flowers perfect, some sterile and highly modified, bracteate and bibracteolate, subsessile in short-pedunculate glomerules. Sepals 5, discrete, hypogynous, concave, subequal, 1–3 ribbed, occasionally pungent. Stamens 5, the filaments flattened and united below into an appendiculate tube; anthers 4-locellate, introrse, medially attached. Ovary ovoid, 1-locular, 1-ovulate; ovules campylotropous on elongate flattened funicles; style 1, filiform; stigma 1, capitate. Fruit an ovoid indehiscent utricle; seeds cochleate-orbiculate, succineous. Pubescent branched ascending to prostrate occasionally frutescent herbs. Leaves opposite, entire, petiolate, strigose, deciduous. Inflorescences spicate, composed of terminal and axillary thyrses of complex glomerules containing some highly modified flowers with some of the bracts and sepals uncinate-spinescent.

Of this rather weedy genus of some twenty species, most of the species are centered in Africa and the Orient. Only two occur in Central America, usually in disturbed habitats of low elevations, where they may become annoying weeds.

a. Terminal spikes 2–10 times as long as the uppermost leaves, interrupted over half their length; lower glomerules with mostly 3 fertile flowers and around 40 uncinate structures 1–2 mm. long; seeds 1–1.5 mm. broad; sepals 2–3 mm. long; pseudostaminodia 3-toothed..... 1. C. PROSTRATA

aa. Terminal spikes 1–2 times as long as the uppermost leaves, interrupted less than half their length; lower glomerules with 1 fertile flower and around 12 uncinate structures 1–4 mm. long; seeds 1.5–2 mm. broad; sepals 2.5–4 mm. long; pseudostaminodia irregularly lacerate..... 2. C. ACHYRANTHOIDES

1. CYATHULA PROSTRATA (L.) Blume, Bijdr. Ned. Ind. 549. 1826.

Achyranthes prostrata L. Sp. Pl. ed. 2:296. 1762.
Cyathula geniculata Lour. Fl. Cochinch. 1:102. 1790.
Desmochaeta prostrata DC. Cat. Hort. Monsp. 102. 1813.
Pupalia prostrata Mart. Nova Acta Acad. Leop.-Carol. 13^1:321. 1826.

Erect or decumbent geniculate pubescent perennials to 1 m. high, often rooting at the lower nodes. Leaves strigose on both surfaces, entire or undulate, ovate to obovate, apically acute, basally acute to rounded, 2–6 cm. long, 1–4 cm. broad; petioles 2–8 mm. long. Inflorescences of terminal and axillary spikes of glomerules, the mature glomerule usually consisting of a central terminal perfect flower and 2

lateral perfect flowers, each of the lateral flowers subtended on each side by a cluster of about 20 hooks representing 3 modified flowers, the hooks not conspicuously longer than the glomerule, the peduncle of the glomerule articulated near the pubescent primary rhachis; spikes 5–30 cm. long, 4–7 mm. broad, with only the distal half continuous. Unmodified flowers perfect; bracts and bracteoles subequal, ovate, mucronate or aristate, 1–1.5 mm. long; sepals 5, subequal, ovate, concave, scariose, pubescent throughout their length, with 1–3 ribs strongly exserted dorsally, 2–3 mm. long; stamens 5, 1–2 mm. long, united below to form a tube bearing 5 intercalated 3-dentate pseudostaminodia; ovary at first tympaniform, becoming ovoid; style 1, stigma 1, at anthesis about equaling the stamens. Utricle ovoid, inconspicuously operculate, 1–2 mm. long; seeds cochleate-orbiculate, succineous, smooth 1–1.5 mm. long.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1357*; Water Valley, vicinty of Chiriquí Lagoon, *von Wedel 1696A*; Bastimentos, Mariano Creek, vicinity of Chiriquí Lagoon, *von Wedel 2898*.

Probably adventive in the Americas where it has a rather spotty distribution, this species is presumed to be native in tropical Asia and Africa. The glomerules are similar in complexity to the spikelets of some grasses, and they probably cling rather tenaciously to fur and clothing

Fig. 116. *Cyathula prostrata*

2. CYATHULA ACHYRANTHOIDES (HBK.) Moq. in DC. Prodr. 13²:326. 1849.

Desmochaeta achyranthoides HBK. Nov. Gen. & Sp. 2:210. 1817.
Desmochaeta densiflora HBK. loc. cit. 211. 1817.
Desmochaeta uncinata R. & S. Syst. Veg. 5:554. 1819.
Pupalia densiflora Mart. Nov. Gen. & Sp. 2:61. 1826.
Cyathula achyranthoides β glabrescens Moq. in DC. Prodr. 13²:327. 1849.
Cyanthula achyranthoides γ densiflora Moq. loc. cit. 327. 1849.
Achyranthes hirtiflora A. Rich. in Sagra, Hist. Cuba 11:175. 1850.
Cyathula prostrata β achyranthoides O. Ktze. Rev. Gen. 542. 1891.

Erect or decumbent geniculate pubescent or glabrate annuals or perennials to 1 m. high, often rooting at the lower nodes. Leaves usually strigose on both surfaces, entire or slightly undulate, ovate to rhombic-ovate, apically acuminate to attenuate, basally acute to cuneate, 4–15 cm. long, 1.5–5 cm. broad; petioles 2–10 mm. long. Inflorescences of terminal and axillary spikes of glomerules, the mature glomerule usually consisting of a fertile lower flower and a rudimentary, rarely perfect, terminal flower with 2 of its sepals uncinate-aristate, the terminal flower subtended on each side by a cluster of 3–7 hooks representing 1 modified flower, some of the hooks conspicuously longer than the glomerule; spikes 3–15 cm. long, 5–7 mm. broad, interrupted less than half their length; bracts and bracteoles subequal, ovate, concave, mucronate or aristate, 1.5–3 mm. long; sepals 5, subequal, ovate, concave, scariose, usually pubescent only at the extremities, with 1–3 ribs occasionally strongly exserted dorsally, 2.5–4 mm. long, 1–1.5 mm. broad; stamens 5, 1–2 mm. long, united below forming a tube bearing 5 intercalated irregularly lacerate pseudostaminodia; ovary at first tympaniform, becoming ovoid; style 1, stigma 1, at anthesis about equaling the stamens. Utricle ovoid, rather conspicuously operculate, 1.5–2.5 mm. long; seeds cochleate-orbiculate, succineous, smooth, 1.5–2.5 mm. long.

BOCAS DEL TORO: vicinity of Nievecita, ca. 0–50 m., *Woodson, Allen & Seibert 1806*; Little Bocas, vicinity of Chiriquí Lagoon, *von Wedel 2525*: Peach Creek, vicinity of Chiriquí Lagoon, *von Wedel 2650*; Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 610 & 1142*. CANAL ZONE: shrubby grassy trail-border, *MacBride & Featherstone 2779*; Balboa Heights, *Greenman & Greenman 5038*. COLÓN: Juan Mina plantation, Río Chagres, region above Gamboa, 25 m., *Allen 4119*. DARIÉN: trail between Paya and Pucro, *Stern, Chambers et al. 402A*; vicinity of Boca de Cupe, ca. 40 m., *Allen 891*. VERAGUAS: between R. Tabasará and Soná on highway, *Woodson, Seibert & Allen 504*.

Extending from Mexico and the West Indies to Brazil, this species is rather common in low-elevation disturbed habitats of tropical America. In Guatemala it is called *cola de armado* and in Honduras, *mozote*. The stouter hooks of the glomerules of this species may perhaps make them more painful and tenacious clingers than those of the preceeding species.

7. PFAFFIA Mart.

PFAFFIA Mart. Nov. Gen. & Sp. 2:20. 1826.

Serturnera Mart. loc. cit. 36. 1826.
Hebanthe Mart. loc. cit. 42. 1826.

Flowers normally perfect, bracteate and bibracteolate, sessile, often with an unpleasant odor. Sepals 5, discrete, hypogynous, concave, subequal, the outer 3 slightly larger, often 3-ribbed, greenish white, becoming scariose, with a conspicuous tuft of intertwined whitish hairs arising mostly within and longer than the outer sepals. Stamens 5, the filaments flattened and united below forming an entire or appendiculate tube; anthers 2-locellate, introrse, medially attached. Ovary ovoid to obovoid, 1-locular, 1-ovulate; ovules campylotropous on elongate flattened funicles; style 1, very short; stigma 1, bilabiate, exceeding the style. Fruit an indehiscent utricle; seeds cochleate-orbiculate, reddish brown. Subglabrous or copiously pubescent clambering vines or erect shrubs. Leaves opposite, entire to undulate, subsessile to short petiolate, glabrate to densely pubescent. Inflorescences paniculate with opposite branches or verticillate branches ultimately bearing spikes. (In some South American species, the inflorescence consists of condensed terminal heads.)

Of this predominantly South American genus of some twenty species, two members of the clambering section HEBANTHE are found in Panama, one apparently reaching its northernmost station here. Stützer in a generic monograph (in Rep. Spec. Nov. Beih. 88:2. 1935) has noted that the section HEBANTHE is closer related to *Iresine* § TROMMSDORFFIA than to the other two sections of the genus *Pfaffia*.

a. Mature sepals 2–3.5 mm. long, the ribs often not obvious to the naked eye; rhachises and lower leaf surfaces densely rufous-pubescent; stamen tube entire..... 1. P. GRANDIFLORA

aa. Mature sepals 1.5–2.5 mm. long, the ribs obvious to the naked eye; rhachises and lower leaf surfaces slightly cinereous-pubescent; stamen tube with 2 rounded teeth between adjacent filaments..... 2. P. PANICULATA

1. PFAFFIA GRANDIFLORA (Hook.) R. E. Fr. in Ark. Bot. 16^{12}:10. 1921.

Iresine grandiflora Hook. in Icon. Pl. 2: tab. 102. 1837.
Gomphrena paniculata var. γ *hookeriana* Seub. in Mart. Fl. Bras. 5^{1}:192. 1875.
Hebanthe decipiens Hook. f. in Benth. & Hook. f. Gen. Pl. 3:41. 1880.
Hebanthe hookeriana Hems. Biol. Cent. Am. 3:19. 1882.
Gossypianthus hookerianus O. Ktze. Rev. Gen. 543. 1891.
Gossypianthus decipiens O. Ktze. loc. cit. 543. 1891.
Pfaffia hookeriana (Hems.) Greenm. in Field Mus. Bot. 2:330. 1912.
Pfaffia grandiflora (Hook.) R. E. Fr. in Stützer, in Rep. Spec. Nov. Beih. 88:9. 1935.
Pfaffia grandiflora var. *hookeriana* Stützer, loc. cit. 10. 1935.

Suffrutescent, usually pubescent, clambering perennials to about 3 m. long. Leaves rufous-strigose, at least below, lanceolate to broadly ovate, apically acute to attenuate, basally rounded to acute, 2–10 cm. long, 1–5 cm. broad; petioles 2–10 mm. long. Inflorescence a terminal panicle of pedunculate, opposite or verticillate, simple or compound spikes, the lower often subtended by reduced leaves, the rhachises and peduncles densely rufous-pubescent. Flowers perfect, often infertile, sessile; bracts and bracteoles subequal, broadly ovate, rufous-tomentose, 1–2 mm. long, 1–2 mm. broad; sepals 5, subequal, elliptic, the ribs obscured by the pubescence, 2–3.5 mm. long, 1–2 mm. broad; stamens 5, 1.5–2.5 mm. long, united below into an exappendiculate tube about 0.5 mm. long; ovary

at anthesis ovoid; stigma 1, bilabiate, subsessile. Fruit an included indehiscent utricle to 2 mm. long; seeds cochleate-orbiculate, reddish brown, about 1.5 mm. long, on a funicle up to 1 mm. long.

DARIÉN: Cana and vicinity, 2000–6500 ft., *Williams 828*.

This species ranges from Mexico to British Guiana and Peru. Standley (in Contr. U. S. Nat. Herb. 27:174. 1928) reports this species, as *P. hookeriana* (Hems.) Greenm., to have been collected at Gatuncillo. His identification is questionable however since he keys the species as having lobed stamen tubes. The reliability of pseudostaminodial characters is thrown open to suspicion by examination of *Williams 828* from Darién. In this specimen, possibly a hybrid between *P. grandiflora* and *P. paniculata*, although leaning strongly toward the former in other characters, the stamen tube in a single flower has pseudostaminodia between some filaments and none between others. Both Fries (in Ark. Bot. 16^{12}:10. 1921) and Standley (in Field Mus. Bot. 13:490. 1936) have erroneously associated the name *P. grandiflora* (Hook.) R. E. Fr. with *P. brachiata* Chod. (incl. *P. hangii* R. E. Fr.), a species differing by its striking dendroid pubescence.

2. PFAFFIA PANICULATA (Mart.) O. Ktze. Rev. Gen. 542. 1891.

Iresine erianthos Poir. in Lam. 3: suppl. 180. 1813.
Hebanthe paniculata Mart. Nov. Gen. & Sp. 2:140. 1826.
Hebanthe virgata Mart. loc. cit. 143. 1826.
Iresine paniculata Spreng. Syst. Veg. Cur. Post. 103. 1827.
Gomphrena paniculata Moq. in DC. Prodr. 13^2:385. 1849.
Xerea paniculata O. Ktze. Rev. Gen. 545. 1891.
Pfaffia eriantha (Poir.) O. Ktze. loc. cit. 543. 1891.

Suffrutescent subglabrous clambering perennials to about 3 m. long. Leaves glabrous to appressed strigose below, lanceolate to ovate, apically acute, basally rounded to cuneate, 2–8 cm. long, 1–4 cm. broad; petioles 2–7 mm. long. Inflorescence a terminal panicle of pedunculate, opposite or verticillate, simple or compound spikes, the lowermost often subtended by reduced leaves, the rhachises and peduncles slightly cinereous-pubescent. Flowers perfect, often infertile, sessile, bracts and bracteoles subequal, broadly ovate, translucent except for the carinae, 1–1.5 mm. long, 1–2 mm. broad; sepals 5, subequal, elliptic, the outer 3 conspicuously 3-ribbed, 1.5–2.5 mm. long, 1–1.5 mm. broad; stamens 5, 1.5–2 mm. long, united below into a tube with 2 rounded lobes between adjacent filaments, the tube about 0.5 mm. long; ovary at anthesis obovoid, occasionally distally 4-lobate; stigma 1, bilabiate, subsessile. Fruit an included indehiscent utricle about 1 mm. long; submature seeds cochleate-orbiculate, reddish brown, about 0.5 mm. broad, on funicles about 1 mm. long.

COCLÉ: El Valle, floor, 1800 ft., *Allen 4475*.

This species, far from its reported range of Brazil to Peru and Paraguay, is possibly a recent introduction in Panama. The conspicuous cottony mass of hairs are certainly an aid to fruit dispersal. Three recent works on *Pfaffia* (Fries, in Ark. Bot. 16^{12}:1. 1921; Suessenguth in Rep. Sp. Nov. 35:325. 1934; and Stützer, in

Fig. 117. *Pfaffia paniculata*

Rep. Sp. Nov. Beih. 88:1. 1935) all recognize that *P. eriantha* was described from a monstrosity. This monstrosity, which occurs in at least three species, has many or all of the flowers reduced to small sterile clusters of short stout hairs. However any flowers that may develop normally are adequate for identification. Moquin (in DC. Prodr. 13^2:386. 1849), who examined the type of *P. eriantha*, gives a description adequate to identify it with *P. paniculata*. International rules of nomenclature recommend that names based on monstrosities be rejected; therefore the name *P. paniculata* is upheld.

8. IRESINE P. Br.

IRESINE P. Br. Hist. Jam. 358. 1756.

Trommsdorffia Mart. Nov. Gen. & Sp. 2:40. 1826.
Rosea Mart. loc. cit. 58. 1826.
Xerandra Raf. Fl. Tell. 3:43. 1837.
Ireneis Moq. in DC. Prodr. 13^2:349. 1849.

Flowers perfect, polygamous or dioecious, bracteate and bibracteolate, subsessile in spikes or glomes. Sepals 5, discrete, hypogynous, concave, subequal, becoming scariose, often with conspicuous tufts of hairs between the sepals and the bracteoles. Stamens 5, the filaments flattened and united below into an entire or appendiculate tube; anthers bilocellate, oblong, introrse, medially attached. Ovary 1-locular, 1- ovulate; ovule campylotropous on an elongate flattened funicle; stigmata 2–3, filiform or deltoid. Fruit an indehiscent utricle; seeds cochleate-orbiculate, whitish or reddish brown, smooth. Glabrous to copiously pubescent herbs, shrubs, trees or clambering vines. Leaves opposite, entire to denticulate, petiolate, glabrous to sericeous, herbaceous to coriaceous. Inflorescences of spikes or glomes, paniculately disposed, the branching alternate, opposite or verticillate.

This heterogeneous genus, of some forty species, is largely if not wholly native to the Americas. I have seen no specimens, except of the cultivant *Iresine herbstii* Hook., from outside the Americas and the West Indies. *Iresine herbstii* is cultivated in many places for its attractive variegated red and yellow foliage, but I have seen no specimens from Panama. The genus, and especially the polygamous and dioecious species, are sorely in need of revision. Four species are known to occur in Panama.

a. Flowers perfect or polygamous; spikes ovoid or globose, pedunculate, alternate, opposite or verticillate on the rhachis; seeds whitish or reddish brown; style about half as long as the stigmata; herbaceous or suffruticose perennials, often clambering.
  b. Leaves near the inflorescence ovate or elliptic, their petioles amplexicaul; spikes mostly opposite or verticillate; rhachises obviously cinereous-pubescent; stigmata deltoid, scarcely reflexed; seeds whitish.
    c. Leaves densely pubescent below; intrafloral hairs about equaling the calyx; pseudostaminodia bilobate; utricle 1–1.3 mm. long..... 1. I. HASSLERIANA
    cc. Leaves sparsely strigose below; intrafloral hairs about twice as long as the calyx; pseudostaminodia deltoid or absent; utricle 1.5–2 mm. long..... 2. I. COMPLETA
  bb. Leaves near the inflorescence linear or lanceolate, their petioles mostly not amplexicaul; spikes mostly alternate; rhachises glabrate or obscurely puberulent; stigmata filiform, ultimately reflexed; seeds reddish brown..... 3. I. ANGUSTIFOLIA
aa. Flowers strictly dioecious; spikes filiform or narrowly pyramidal, mostly sessile, alternate on the rhachis; seeds reddish brown; style obsolete, less than a third as long as the filiform stigmata; herbaceous upright or ascending perennials..... 4. I. CELOSIA

1. IRESINE HASSLERIANA Chod. in Bull. Herb. Boiss. 2^3:390. 1903.

Iresine macrophylla R. E. Fr. in Ark. Bot. 16^{12}:41. 1921.

Erect or clambering shrubs, the younger branches cinereous-pubescent. Leaves

Fig. 118. *Iresine hassleriana*

herbaceous to coriaceous, appressed pubescent below, glabrate above, narrowly elliptic to ovate, apically acute to attenuate and mucronate, basally rounded to acute, 2–15 cm. long, 1–8 cm. broad; petioles 3–15 mm. long. Inflorescence a panicle of opposite or verticillate pedunculate glomes, the rhachises cinereous-pubescent. Flowers perfect, the bracts and bracteoles subequal, orbicular, apically rounded, concave, entire, transparent, 1–1.5 mm. long, with a conspicuous tuft of hairs about equaling the sepals in length and arising between the bracts and the sepals; sepals 5, subequal, oblong-ovate, acute, obscurely 3–5 nerved, 1.5–2 mm. long; stamens 5, united below into a shallow tube bearing two rounded lobes between adjacent filaments; ovary subglobose; style 1, shorter than the 2 deltoid stigmata. Fruit an indehiscent ovoid utricle, 1–1.3 mm. long; seeds whitish, cochleate-orbiculate, about 1 mm. long.

PROVINCE UNKNOWN: *Sutton Hayes 934.*

Apparently reaching its northern limits in Panama, this species is also found in

Peru, Bolivia, Brazil and Colombia. Specimens from the northern half of the range tend to have smaller less coriaceous leaves. *Iresine domingensis* Urban, described from Haiti, is a very closely related species, which Suessenguth (in Rep. Sp. Nov. 35:320. 1934) reports from Trinidad and Venezuela.

2. IRESINE COMPLETA Uline & Bray, in Bot. Gaz. 21:349. 1896.

Erect or clambering shrubs, the younger branches cinereous-pubescent. Leaves herbaceous, glabrate or scantily strigose below, ovate, apically attenuate and mucronate, basally acute, 1.5–11 cm. long, 1–5.5 cm. broad; petioles 4–10 mm. long. Inflorescence a panicle of opposite or verticillate pedunculate glomes, the rhachises cinereous-pubescent. Flowers perfect (or polygamous?); bracts and bracteoles subequal, broadly ovate, acute, concave, entire, transparent, about 1 mm. long, with a conspicuous tuft of septate hairs about twice as long as the sepals arising between the bracts and the sepals; sepals 5, subequal, oblong-ovate, acute, obscurely 3-nerved, 2–2.5 mm. long; stamens 5, united below into a shallow tube bearing obscure broadly deltoid pseudostaminodia between adjacent filaments; ovary subglobose; style 1, slightly shorter than the 2 deltoid stigmata. Fruit an indehiscent ovoid utricle, 1.5–2 mm. long; seeds whitish, cochleate-orbiculate, about 1.5 mm. long.

DARIÉN: above Paca and near Cana, *Williams 706*.

Ranging from Panama to Guatemala, this species is nowhere commonly collected. The cited specimen, annotated by Standley, agrees with the original descriptions in all respects except that the pseudostaminodia are not prominent. Uline & Bray (in Bot. Gaz. 21:349. 1896) have emphasized that the type, *Thieme 338*, collected in 1888, is completely hermaphroditic. Donnell Smith (Enum. Plant. Guat. 5:72. 1899) cites two of Thieme's collections, omitting Thieme's numbers, and using his own numbers, *5443* collected in 1889 and *5447* collected in 1890, as *Iresine completa*. *Donnell Smith 5447* is however the staminate plant of a dioecious or polygamous species and has obvious pistillodes. It is obviously not the specimen used in the original description. Nevertheless Suessenguth (in Rep. Sp. Nov. 35:320. 1935) offers us his "*Ergänzung zur Originaldiagnose*" citing *Donnell Smith 5447* as the type. This cannot be the holotype because the flowers are not perfect, they lack the basal tuft of hairs and they lack the orbicular utricles. It is possible, but presently strictly conjectural, that *I. completa* is polygamous with the pistillate flowers perfect and the staminate flowers bearing pistillodes.

3. IRESINE ANGUSTIFOLIA Euphr. Beskr. St. Barth. 165. 1795.

Iresine elatior Rich. in Willd. Sp. Pl. 4:766. 1805.
Iresine racemosa Poir. in Lam. Encycl. Suppl. 3:180. 1813.
Rosea elatior Mart. Nov. Gen. & Sp. 2:59. 1826.
Xerandra elatior Raf. Fl. Tell. 3:43. 1837.
Alternanthera linearis Bello, in Anal. Soc. Esp. Hist. Nat. 12:107. 1883.

Erect or reclining suffruticose perennials to 1 m. high, the younger branches glabrous or scantily strigose below, lanceolate to narrowly ovate, apically attenuate and mucronate, basally acute to attenuate, 5–10 cm. long, 0.5–3 cm. broad; petioles 0.5–2 cm. long. Inflorescence a panicle of alternate pedunculate ovoid spikes, these occasionally subtended by reduced linear leaves, the rhachises glabrate or puberulent. Flowers perfect, the bracts and bracteoles subequal, broadly ovate, mucronate, concave, entire, transparent, 0.5–1 mm. long, with a conspicuous mass of tawny hairs arising between the bracts and the sepals; sepals 5, subequal, oblong-ovate, acute 3-nerved, 1–1.5 mm. long; stamens 5, united below into a shallow tube with obsolete pseudostaminodia; ovary obovoid; style 1, slightly shorter than the 2 papillose filiform stigmata. Fruit an indehiscent utricle, 0.5–1 mm. long; seeds reddish brown, cochleate-orbiculate, 0.6–0.8 mm. broad.

DARIÉN: Río Sabana, *Leopold 131*; Boca de Cupe, *Williams 670*.

This lochmocolous species extends from Mexico through Central America to Brazil and Ecuador. Standley (in Contr. U. S. Nat. Herb. 27:174. 1928) reports that the name *cadillo*, a name applied to many plants with bur-like fruits, is used on Taboga Island.

4. IRESINE CELOSIA L. Syst. ed. 10:1291. 1759.

Celosia paniculata L. Sp. Pl. 206. 1753.
Iresine celosioides L. Sp. Pl. ed. 2:1456. 1763.
Iresine diffusa Humb. & Bonpl. in Willd. Sp. Pl. 4:765. 1805.
Iresine elongata Humb. & Bonpl. loc. cit. 765. 1805.
Iresine parviflora HBK. Nov. Gen. & Sp. 2:198. 1818.
Iresine havanensis HBK. loc. cit. 199. 1818.
Iresine mutisii HBK. loc. cit. 200. 1818.
Iresine verticillata Spreng. Syst. 1:821. 1825.
Iresine polymorpha Mart. Nov. Gen. & Sp. 2:56. 1826.
Iresine polymorpha α alopecuroidea Mart. loc. cit. 56. 1826.
Iresine polymorpha β effusa Mart. loc. cit. 56. 1826.
Iresine polymorpha γ verticillata Mart. loc. cit. 56. 1826.
Xerandra celosioides Raf. Fl. Tell. 3:43. 1837.
Iresine floribunda Mart. & Gal. in Bull. Acad. Brux. 101:347. 1843.
Iresine celosioides var. *eriophylla* Benth. Bot. Voy. Sulph. 156. 1844.
Iresine hookeri Moq. in DC. Prodr. 13^2:344. 1849.
Iresine acuminata Moq. loc. cit. 345. 1849.
Iresine celosioides β pubescens Moq. loc. cit. 347. 1849.
Iresine eriophylla Moq. loc. cit. 347. 1849.
Iresine gossypiantha A. Rich. in Sagra, Hist. Cuba 11:177. 1850.
Iresine eriophora Peyr. in Linnaea 30:21. 1850.
Alternanthera paniculata Bello, in Anal. Soc. Esp. Hisp. Nat. 12:106. 1883.
Iresine paniculata (L.) O. Ktze. Rev. Gen. 2:542. 1891. not *I. paniculata* Poir.
Achyranthes lanata Sessé & Moc. Fl. Mex. ed. 2:67. 1894. not *A. lanata* L.
Iresine paniculata var. *floridana* Uline & Bray, in Bot. Gaz. 21:353. 1896.

Erect or clambering herbaceous annuals or perennials, to 3 m. high, the younger branches glabrous or pubescent. Leaves herbaceous, glabrate to densely pubescent, ovate, apically acute to attenuate and mucronate, basally rounded to cuneate, 4–15 cm. long, 1–7 cm. broad; petioles 0.5–6 cm. long. Inflorescence a panicle of subsessile filiform to pyramidal spikes, the rhachises glabrate to densely pubescent.

Flowers dioecious; bracts and bracteoles subequal, broadly ovate, mucronate, concave, often auriculate, transparent, 0.5–1 mm. long, with a conspicuous mass of hairs longer than the sepals arising between the bracts and the sepals of the female flowers; stamens 5, united below into an entire or minutely denticulate tube; ovary obovoid; style minute, much shorter than the 2 (–3) filiform stigmata. Fruit an indehiscent utricle 0.5–1 mm. long; seeds reddish brown, cochleate-orbiculate, 0.5–0.6 mm. broad.

BOCAS DEL TORO: Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 1762 & 1849*. CANAL ZONE: Colon to Empire, Panama Railroad, *Crawford 453*; between Mt. Hope and Santa Rita trail, *Cowell 81*; Chagres, Isthmus of Panama, *Fendler 260*; between Summit and Gamboa, *Greenman & Greenman 5235*. CHIRIQUÍ: Potrero Muleto to Summit, Volcán de Chiriquí, 3500–4000 m., *Woodson & Schery 466*; Río Chiriquí to Remedios, 15–50 m., *Woodson, Allen & Seibert 1192*; Finca Lérida to Boquete, ca. 1300–1700 m., *Woodson, Allen & Seibert 1131*; Bajo Mono, mouth of Quebrada Chiquero, along Río Caldera, 155–2000 m., *Woodson, Allen & Seibert 1012*; Río Chiriquí Viejo Valley between El Volcán and Cerro Punta, *G. White 21*; rain forest, Bajo Chorro, Boquete, 6000 ft., *Davidson 320*; Volcán de Chiriquí, Boquete Distr., 8000 ft., *Davidson 932*; vicinity of New Switzerland, central valley of Río Chiriquí Viejo, 1800–2000 m., *Allen 1411*. COCLÉ: no specified locality, *Macbride 2717*. PANAMÁ: Taboga Island, up to 300 m., *Allen 117*; near mouth of R. Chagres, *Allen 875*; hills between Capire and Potrero, *Dodge & Hunter 8645*. PROVINCE UNKNOWN: *Sutton Hayes 722, 928 & 929*.

This species is rather common in the warmer regions of North, Central and South America. Standley & Steyermark (in Field Mus. Bot. 24[4]:170. 1946) report that the sap is employed as a remedy for erysipelas around Cobán in Guatemala. Maya names for this plant are *zactezxiu* and *zacxiu*. Other vernacular names reported are *pie de paloma, velo de princesa, adorno de niño, chancanil, tabudo, mosquito, hierba de gato, siete pellejos, coyontura, coyontura de pollo, taba de güegüecho* and *camarón*. *Iresine spiculigera* Seub. and *Iresine acicularis* Standl. were first lumped by Suessenguth (in Rep. Sp. Nov. 35:319. 1934), but later separated again (in Rep. Sp. Nov. 39:13. 1935). Standley (in Field Mus. Bot. 13[2]:517. 1937) apparently accepts the lumping and further states that *I. spiculigera* "is doubtfully distinct from *I. celosia*". Analysis of *I. spiculigera* with cinereous spicular pubescence, *I. acicularis*, with ochraceous spicular pubescence, and *I. frutescens* Moq., with small flowers, reveals that they are best considered conspecific with *I. celosia* L.

9. PHILOXERUS R. Br.

PHILOXERUS R. Br. Prodr. 416. 1810.

Caraxeron Vaill. in Raf. Fl. Tell. 3:38. 1837.

Blutaparon Raf. New Fl. 4:45. 1838.

Flowers perfect, bracteate and bibracteolate, subsessile in spikes. Sepals 5, discrete or basally slightly connate, hypogynous, the outer 3 flat and broader, the inner 2 conduplicate and narrower. Stamens 5, the filaments flattened and united below to form a very shallow tube; pseudostaminodia absent; anthers 2-locellate, introrse, medially attached. Ovary ovoid to orbiculate, 1-locular, 1-ovulate;

ovules on elongate flattened funicles; stigmata 2, on 1 short style, often erect at anthesis and recurving in fruit. Fruit an orbiculate indehiscent utricle; seeds cochleate-orbiculate, reddish brown. Prostrate or decumbent glabrous to pubescent herbaceous perennials. Leaves opposite, entire, often succulent, the sessile bases usually amplexicaul. Inflorescences of terminal and axillary pedunculate congested spikes or glomes often subtended by slightly reduced foliar leaves.

This small genus of two or three species seems to be largely restricted to beaches and salt flats in tropical America and west Africa. Schinz (in Engler & Prantl, Pflanzenf. 16c:83. 1934) has suggested that many Australian species formerly referred to this genus perhaps belong to *Gomphrena*. Only one species reaches North America.

1. Philoxerus vermicularis (L.) R. Br. Prodr. 416. 1810.

Gomphrena vermicularis L. Sp. Pl. 224. 1753.
Illecebrum vermiculatum L. Sp. Pl. ed. 2:300. 1762.
Gomphrena aggregata Willd. Enum. 294. 1809.
Philoxerus aggregatus HBK. Nov. Gen. & Sp. 2:203. 1817.
Philoxerus crassifolius HBK. loc. cit. 203. 1817.
Achyranthes vermicularis Ell. Bot. S. C. & Ga. 1:310. 1821.
Gomphrena crassifolia Spreng. Syst. 1:824. 1825.
Caraxeron vermicularis Raf. Fl. Tell. 3:38. 1837.
Blutaparon brevifolium Raf. New. Fl. 4:45. 1838.
Blutaparon repens Raf. loc. cit. 46. 1838.
Iresine vermicularis Moq. in DC. Prodr. 13^2:340. 1849.
Iresine crassifolia Moq. loc. cit. 340. 1849.
Iresine aggregata Moq. loc. cit. 340. 1849.
Cruzeta crassifolia Maza, Fl. Haban. 94. 1897.
Lithophila vermiculata Uline, in Field Mus. Bot. 2:39. 1900.

Prostrate or decumbent perennials, the much branched stems glabrous except at the nodes. Leaves glabrous, succulent, linear to narrowly oblanceolate, apically acute to rounded, often mucronate, basally cuneate, 1–5.5 cm. long, 2–10 mm. broad, the leaf bases encircling the swollen nodes, with an axillary tuft of hairs. Inflorescences of terminal and axillary pedunculate bracteate white to stramineous spikes or glomes, 5–30 mm. long, 5–10 mm. broad, solitary or aggregated, the rhachises villous. Flowers perfect; bracts and bracteoles subequal, ovate, acute to acuminate, concave, translucent, 2–3 mm. long, slightly shorter than or equaling the sepals; sepals 5, the outer 3 almost flat, usually glabrous, apically rounded, 3–4 mm. long, 1–1.5 mm. broad, the inner 2 conduplicate, pubescent, apically acute, 3–4 mm. long, 1 mm. broad; stamens 5, 1–2.5 mm. long, united below into a very shallow or obsolete tube; pseudostaminodia absent; ovary orbiculate to elliptic, style 1, about as long as the 2 papillose stigmata. Fruit an indehiscent utricle, about 2 mm. long; seeds cochleate-orbiculate, reddish brown, 0.8–1.2 mm. broad.

Bocas del Toro: Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 1948*.

A rather characteristic sea beach plant, this species ranges from Florida and Texas to Mexico and British Honduras, and from Panama to Brazil in the Americas; it also occurs on the west coast of Africa. As the name implies, the plant

Fig. 119. *Philoxerus vermicularis*

reputedly possesses vermifuge qualities. *P. portulacoides* St.-Hil. differing in having glabrous white sepals, and *P. littoralis* Suesseng., differing in having glabrous white inner sepals and pilose foliar midribs are weakly defined species occurring in South America.

10. ALTERNANTHERA Forskal

Alternanthera Forskal, Fl. Aeg.-Arab. 28. 1775.

Flowers perfect, bracteate and bibracteolate, sessile or subsessile in spikes or glomes. Sepals 5, discrete, hypogynous, concave, subequal or strongly dissimilar, white to purple, the bases often indurate. Stamens 3–5, the filaments flattened and united below into an entire or appendiculate tube; anthers 2-locellate, oblong, introrse, medially attached. Ovary globose to obovoid, often compressed, 1-locular, 1-ovulate; ovule campylotropous on an elongate funicle; stigma 1, capitate or obscurely bilabiate, on a short or elongate style. Fruit a membranaceous utricle, indehiscent; seeds cochleate-orbicular, smooth. Glabrous to copiously pubescent erect, scandent or prostrate annuals or perennials. Leaves opposite, sessile or petiolate, entire to denticulate, glabrous to densely pubescent, mostly herbaceous. Inflorescences of axillary and terminal sessile or pedunculate spikes or glomes.

This genus of over 100 species is best developed in the Americas, although many species are ubiquitous weeds. Some species are cultivated for their ornamental inflorescences and others are planted as tufted border plants and soil binders. *Alternanthera axillaris* Hornem. and *A. repens* (L.) Gmel. are rather obnoxious weeds with pungent sepals. Working under the American Code of nomenclature, Standley (in Jour. Wash. Acad. 5:72. 1915) explains the rather complicated reasons which led him to transfer the *Alternanthera* species to *Achyranthes*, a treatment which he later abandoned. Hitchcock & Green (in Brittonia 6:114. 1947) have proposed that *Alternanthera repens* (L.) Gmel. be the lectotype of the genus. Eleven species are reported from Panama.

a. Inflorescences sessile in the axils of small leaves (mostly 1–4 cm. long); outer and inner sepals strongly dissimilar, the outer 1.5–2 times as broad as the inner (sepals subequal but exceeded by the utricle in *A. sessilis*); prostrate or decumbent herbs.
  b. Utricle longer than the sepals; sepals subequal acute, 1-nerved, glabrous; pubescence of simple hairs..... 1. A. SESSILIS
  bb. Utricle shorter than the sepals; sepals dimorphic or trimorphic, accuminate to aristate, 3–5 nerved, pubescent; pubescence of stellate or septate hairs.
    c. Filaments longer than the pseudostaminodia; stigmata as long as or longer than the styles, attaining or exceeding the anthers; sepals dimorphic or trimorphic; prostrate plants with the leaves often less than 1.5 cm. long.
      d. Inflorescences subglobose to cylindric; sepals dimorphic, the outer 3 subequal with flexible awns if any, whitish; bracteoles 0.2–0.5 as long as the sepals; stigmata longer than the styles; seeds 1–1.2 mm. broad..... 2. A. POLYGONOIDES
      dd. Inflorescences mostly cylindric; sepals trimorphic, with 2 of the outer 3 aristate with rigid awns, stramineous, the third sepal 0.5–1 mm. shorter, merely acuminate; bracteoles more than half as long as the sepals; stigmata about as long as the styles; seeds 1–1.5 mm. broad..... 3. A. REPENS

cc. Filaments shorter than the pseudostaminodia; stigmata shorter than the styles, exceeded by the anthers; sepals dimorphic; prostrate or decumbent herbs, the leaves often over 1.5 cm. long.

e. Leaves apically acute or acuminate, glabrate or sparsely strigose below..... 4. A. FICOIDEA

ee. Leaves apically rounded, densely cinereous-pubescent below with stellate hairs..... 5. A. HALIMIFOLIA

aa. At least some of the inflorescences pedunculate in the axils of larger leaves (mostly 4–10 cm. long); outer and inner sepals subequal; erect or clambering shrubs or decumbent aquatics.

f. Sepals 5–6 mm. long, 3–4 times as long as the bracts; glomes white, 10–18 mm. broad; peduncles unbranched, mostly less than 5 cm. long; subglabrous herbaceous aquatic plants..... 6. A. PHILOXEROIDES

ff. Sepals 2–6 mm. long, no more than twice as long as the bracts; inflorescences white to purple, 4–12 mm. broad; peduncles branched or unbranched, 1–9 cm. long; glabrate to densely pubescent suffruticose terrestrial plants.

g. Glomes 9–12 mm. broad, if narrower, subsessile; sepals 4–6 mm. long.

h. Peduncles mostly simple and exceeded by the subtending leaves; leaves ovate, short-strigose or glabrate; sepals short-strigose, the hairs mostly less than 2 mm. long; styles 1–2 times as long as the stigmata; pseudostaminodia almost as long as the sepals..... 7. A. WILLIAMSII

hh. Peduncles mostly trichotomously branched and exceeding the subtending leaves; leaves lanceolate, sericeous below; sepals pubescent with long beaded hairs, many of the hairs 3–5 mm. long; styles 2–3 times as long as the stigmata; pseudostaminodia about half as long as the sepals..... 8. A. LAGUROIDES

gg. Spikes 4–7 mm. broad, pedunculate; sepals 2–3.5 mm. long.

i. Leaves linear to linear-elliptic, 2.5–5 cm. long, 3–6 mm. broad; peduncles unbranched; flowers stramineous..... 9. A. STENOPHYLLA

ii. Leaves ovate to elliptic, 2.5–10 cm. long, 6–50 mm. broad; peduncle branched or unbranched; flowers white, stramineous or purple.

j. Peduncles unbranched; flowers white to stramineous; seeds reddish brown; styles about twice as long as the stigmata..... 10. A. MEXICANA

jj. Peduncles branched; flowers purplish; seeds reddish brown to black; styles about as long as the stigmata..... 11. A. PANAMENSIS

1. ALTERNANTHERA SESSILIS (L.) R. Br. Prodr. 417. 1810.

Gomphrena sessilis L. Sp. Pl. 225. 1753.
Illecebrum sessile L. Sp. Pl. ed. 2:300. 1762.
Illecebrum indicum Houtt. Nat. Hist. 2:7. 1777.
Alternanthera triandra Lam. Encycl. 1:95. 1783.
Alternanthera denticulata R. Br. Prodr. 417. 1810.
Alternanthera nodiflora R. Br. loc. cit. 417. 1810.
Allaganthera forskalli Mart. Pl. Hort. Erlang. 69. 1814.
Paronychia sessilis Desf. Tabl. Bot. ed. 2:54. 1815.
Adenogramma oppositifolia Hassk. in Flora 31:754. 1851.
Alternanthera tenuissima Suesseng. in Bot. Arch. 39:382. 1939.

Prostrate or decumbent puberulent or glabrous annuals or perennials, the sparsely branched stems to 60 cm. long. Leaves glabrous or sparsely villous below,

elliptic, apically acute and mucronate, basally cuneate to attenuate, 1–4 cm. long, 0.5–1.5 cm. broad; petioles 1–5 mm. long, often winged. Inflorescences of white or pinkish globose heads, 2–4 mm. long, 2–4 mm. broad, sessile in the axils. Flowers perfect, the bracts and bracteoles subequal, acute, 1 mm. long or less; sepals 5, subequal, transparent, not indurate, 1-nerved, slightly concave, 1–1.5 mm. long; stamens 5, united below into a short tube, the pseudostaminodia entire, exceeded by the anthers, about equaling the filaments; ovary obovoid, style 1, 3–4 times as long as the minute capitate stigma. Fruit an indehiscent obcordate yellowish utricle, 1.5–2 mm. long, usually slightly exceeding the sepals; seeds yellowish or reddish brown, cochleate-orbicular, 1–1.2 mm. broad.

This pan-tropical weed seems to range from Honduras to Brazil in the Americas. It inhabits open moist areas and may grow as an aquatic, in which case the vegetative portions are unusually large.

2. ALTERNANTHERA POLYGONOIDES (L.) R. Br. Prodr. 417. 1810.

Gomphrena polygonoides L. Sp. Pl. 225. 1753.
Illecebrum polygonoides L. Sp. Pl. ed. 2:300. 1762.
Achyranthes polygonoides (L.) Lam. Encycl. 1:547. 1785.
Bucholzia polygonoides Mart. Nov. Gen. & Sp. 2:51. 1826.
Alternanthera paronychioides St. Hil. Voy. Distr. Diam. 2:439. 1833.
Steiremis repens Raf. Fl. Tell. 3:41. 1837.
Telanthera polygonoides Moq. in DC. Prodr. 13^2:363. 1849.
Alternanthera ficoidea Griseb. Fl. Brit. W. Ind. 67. 1859. not *Gomphrena ficoidea* L.

Procumbent villous or glabrate perennials, the much branched stems to 80 cm. long. Leaves villous or glabrate, elliptic to ovate or obovate, apically acute to rounded and mucronate, basally cuneate to attenuate, 1–3 cm. long, 0.5–1.5 cm. broad; petioles 2–10 mm. long, often winged and with basal tufts of dentate hairs. Inflorescences of white globose to cylindric heads, 4–10 mm. long, 3–6 mm. broad, sessile in the axils. Flowers perfect, the bracts and bracteoles subequal, acute, ovate, 1–1.5 mm. long; sepals 5, the outer 3 broader, 3-nerved, slightly indurate, pilose below, acuminate, 3–4 mm. long; stamens 5, united below into a short tube, the pseudostaminodia dentate, much exceeded by the anthers; ovary obovoid, style 1, about half as long as the capitate stigma. Fruit an indehiscent obcordate to orbicular utricle, 1–1.5 mm. long; seeds reddish brown, often strongly reticulate, 1–1.2 mm. broad.

This species, occasionally adventive in eastern United States, ranges from Mexico to Argentina in open dry to moist habitats. Standley (in Contr. U. S. Nat. Herb. 27:174. 1928) reports it from Panama but since he keys it as having simple pubescence, the identity of the specimen or specimens is questionable. Backer (in Fl. Mal. 1^4:93. 1949) seems to have lumped this species with *A. ficoidea* (L.) R. Br., but the staminodial differences between the two species appear to be constant. Standley (in Field Mus. Bot. 18:419. 1937) reports the vernacular name *golondrina* in Costa Rica. The South American species *Alternanthera boliviana* Rusby is a very closely allied species, with acute sepals and unusually long spikes.

3. ALTERNANTHERA REPENS (L.) Gmel. Linn. Syst. Nat. ed. 13^2:106. 1791.

Achyranthes repens L. Sp. Pl. 205. 1753.
Alternanthera achyranth. Forsk. Fl. Aeg.-Arab. 28. 1755.
Illecebrum achyrantha L. Sp. Pl. ed. 2:299. 1762.
Achyranthes mucronata Lam. Encycl. 1:547. 1785.
Achyranthes radicans Cav. Anal. Ci. Nat. 3:27. 1801.
Paronychia achyrantha Desf. Tabl. Bot. ed. 2:54. 1815.
Pityranthus crassifolius Mart. Denks. Akad. Munch. 5:179. 1817.
Alternanthera villiflora Scheele, in Linnaea 22:149. 1849.
Alternanthera parviflora Fawc. & Rendle, Fl. Jam. 3:139. 1914.

Procumbent villous or glabrate perennials, the much branched stems up to 50 cm. long. Leaves appressed villous or glabrate, ovate to obovate, apically acute to rounded and mucronate, basally rounded to attenuate, 5–25 mm. long, 3–15 mm. broad; petioles 2–10 mm. long, often winged. Inflorescences of yellowish or stramineous usually cylindric heads, 5–12 mm. long, 4–8 mm. broad, sessile in the axils. Flowers perfect, the bracts and bracteoles subequal, 3–4 mm. long; sepals 5, trimorphic, the outer 2 broader, strongly 3-nerved, indurate, pilose below and with rigid awns, the third sepal narrower, shorter and merely acuminate, the inner 2 conduplicate; stamens 5, united below into a shallow tube, the pseudostaminodia entire or dentate, exceeded by the anthers; ovary obovoid, style 1, about as long as the minute capitate stigma. Fruit an indehiscent obcordate utricle, 1.2–1.5 mm. long; seeds reddish brown, 1–1.5 mm. broad, cochleate-orbicular.

Presumably a native of tropical America, this weedy species is now also well established in Asia, Europe and the East Indies. Standley's recount of the distribution (in N. Am. Flora 21:136. 1916) indicates that the species has been collected in Panama. It certainly is to be expected there. In the Yucatan the Mayas apply the name *cabalxtez*; in Guatemala the names *sanguinaria, sacachiquim* and *hierba de toro* are reported. This species is doubtfully distinct from *A. pungens* HBK., which differs in having subrotund leaves and longer less villous sepals.

4. ALTERNANTHERA FICOIDEA (L.) R. Br. Prodr. 1:417. 1810.

Gomphrena ficoidea L. Sp. Pl. 225. 1753.
Illecebrum ficoideum L. Sp. Pl. ed. 2:300. 1762.
Paronychia ficoidea Desf. Tabl. Bot. ed. 2:14. 1815.
Bucholzia polygonoides α erecta Mart. Nov. Gen. & Sp. 2:51. 1826.
Bucholzia polygonoides β diffusa Mart. loc. cit. 51. 1826.
Bucholzia polygonoides γ radicans Mart. loc. cit. 51. 1826.
Bucholzia ficoidea Mart. loc. cit. 52. 1826.
Steiremis ficoidea Raf. Fl. Tell. 3:41. 1837.
Teleianthera manillensis Walp. in Nov. Act. Ac. Nat. Cur. 19: suppl. 1:404. 1843.
Telanthera polygonoides α diffusa Moq. in DC. Prodr. 13^2:364. 1849.
Telanthera polygonoides β brachiata Moq. loc. cit. 364. 1849.
Alternanthera polygonoides Griseb. Fl. Brit. W. Ind. 67. 1859. not *Gomphrena polygonoides* L.
Alternanthera polygonoides β glabrescens Griseb. loc. cit. 67. 1859.
Alternanthera versicolor Hort. ex Regel, Gartenfl. 101. 1869.
Alternanthera bettzickianna Nich. Gard. Dict. ed. 1:59. 1884.
Alternanthera amoena Back. & Sloot. Handb. Thee. 108. 1924.

Procumbent or decumbent hispidulous or glabrate perennials, the branching stems to 100 cm. long. Leaves slightly pubescent but soon glabrate, elliptic to broadly ovate or obovate, apically acuminate to acute and mucronate, basally rounded to cuneate, 2–6 cm. long, 0.5–2 cm. wide; petioles 2–10 mm. long, usually winged. Inflorescences of stramineous to white globose to ovoid heads, 3–10 mm. long, 3–6 mm. broad, sessile in the axils. Flowers perfect, bracts and bracteoles subequal, ovate, aristate, 1.5–3 mm. long; sepals 5, the outer 3 broader, 3-ribbed, basally indurate and hispidulous, 3–5 mm. long; stamens 5, united below into a tube, the pseudostaminodia lacerate and exceeding the filaments; ovary obovoid; style 1, 2–3 times as long as the capitate stigma. Fruit an indehiscent suborbicular utricle, 1–1.5 mm. long; seeds reddish brown, cochleate-orbiculate, 0.8–1.2 mm. broad.

CANAL ZONE: vicinity of Monkey Hill, *Cowell 33*; Gatún, *Sutton Hayes 185*; near Culebra, 50–200 m., *Pittier 2289*; Chagres, Isthmus of Panamá, *Fendler 261*; Ancón, *Greenman & Greenman 5018*; low ground, outskirts of Ancón, *Greenman & Greenman 5047*; near Corrosion Laboratory, vicinity of Miraflores Locks, *Stern, Chambers et al. 65*. CHIRIQUÍ: vicinity of San Bartolomé, Peninsula de Burica, 0–50 m., *Woodson & Schery 941*. PROVINCE UNKNOWN: *Sutton Hayes 940*.

The native range of this species is perhaps from Mexico to Argentina, but various forms are cultivated elsewhere as ornamentals and soil binders.

5. ALTERNANTHERA HALIMIFOLIA (Lam.) Standl. in Pittier, Pl. Us. Venez. 145. 1926.

Achyranthes halimifolia Lam. Encycl. 1:547. 1785.
Illecebrum frutescens L'Her. Stirp. Nov. 75. 1788.
Illecebrum limense Dum.-Cours. Bot. Cult. 1:646. 1802.
Paronychia frutescens Desf. Tabl. Bot. ed. 2:54. 1815.
Telanthera crucis Moq. in DC. Prodr. 13^2:362. 1849.
Telanthera frutescens Moq. loc. cit. 365. 1849.
Telanthera frutescens β acutifolia Moq. loc. cit. 366. 1849.
Alternanthera ficoidea γ halimifolia (Lam.) O. Ktze. Rev. Gen. 539. 1891
Telanthera flavogrisea Urban, Symb. Ant. 1:300. 1899.
Alternanthera asterotricha Uline, in Field. Mus. Bot. 1:419. 1899.
Alternanthera flavogrisea Urban, Symb. Ant. 5:340. 1907.
Alternanthera crucis Boldingh, Fl. Dutch W. I. 1:58. 1909.
Telanthera halimifolia A. Stewart, in Proc. Calif. Acad. 4^1:58. 1911
Alternanthera ficoidea var. *flavogrisea* Fawc. & Rendle, Fl. Jam. 3:140. 1914.

Procumbent or decumbent sericeous perennials, the sparingly branched stems to 20 cm. long. Leaves densely pubescent with stellate hairs, rarely glabrate, elliptic to ovate, apically rounded and mucronate, basally rounded to cuneate, 1–5 cm. long, 0.5–2.5 cm. broad; petioles 2–10 mm. long. Inflorescences of stramineous ovoid heads, 4–12 mm. long, 3–5 mm. broad, sessile in the axils. Flowers perfect; bracts and bracteoles subequal, ovate, acuminate to aristate, 1–3 mm. long; sepals 5, the outer 3 broader, 3-ribbed, basally indurate and hispidulous, 3–5 mm. long; stamens 5, united below into a tube, the pseudostaminodia lacerate and exceeding the filaments; ovary globose to obovoid; style 1, about twice as long as the capitate stigma. Fruit an indehiscent globose utricle 1–1.5 mm. long; seeds reddish brown, cochleate-orbicular, 0.8–1.1 mm. broad.

Inhabiting woods, thickets, pond borders and sea beaches, mostly at low elevations, this species extends from Mexico and the West Indies to Colombia, Chile and the Galapagos Islands. Standley (in N. Am. Flora 21:140. 1917) indicates that it occurs in Panama. The obvious silvery pubescence usually separates this from the preceding species with which it reputedly intergrades.

6. ALTERNANTHERA PHILOXEROIDES (Mart.) Griseb. Abh. Ges. Wiss. Gött. 24: 36. 1879.

Bucholzia philoxeroides Mart. Nova Acta Acad. Leop.-Carol. 13^1:315. 1826.
Telanthera philoxeroides Moq. in DC. Prodr. 13^2:362. 1849.
Telanthera philoxeroides α obtusifolia Moq. loc. cit. 363. 1849.
Telanthera philoxeroides β acutifolia Moq. loc. cit. 363. 1849.
Telanthera philoxeroides var. δ *phyllantha* Seub. in Mart. Fl. Bras. 5^1;169. 1875.
Telanthera philoxeroides var. γ *denticulata* Seub. loc. cit. 170. 1875.
Achyranthes philoxeroides (Mart.) Standl. in Jour. Wash. Acad. Sci. 5:74. 1915.

Decumbent or ascending glabrate aquatic perennials, the simple or branched, often fistulose stems to 100 cm. long. Leaves glabrous or glabrate, lanceolate to narrowly obovate, apically rounded to acute, basally cuneate, rarely denticulate, 2–10 cm. long, 0.5–2 cm. broad; petioles 1–3 mm. long. Inflorescences of terminal and occasionally axillary white glomes, 10–18 mm. long, 10–18 mm. broad, the usually unbranched peduncles 1–5 cm. long. Flowers perfect, bracts and bracteoles subequal, ovate, acuminate, 1–2 mm. long; sepals 5, subequal, oblong, apically acute and occasionally denticulate, neither indurate nor ribbed, 5–6 mm. long, 1.5–2.5 mm. broad; stamens 5, united below into a tube, the pseudostaminodia lacerate and exceeding the anthers; ovary reniform, the style about twice as long as the globose capitate stigma. Fruit an indehiscent reniform utricle 1 mm. long, 1–1.5 mm. broad; mature seeds not seen.

Standley (in N. Am. Fl. 21:142. 1917) gives the range of this species as from Colombia to Brazil and Argentina, adventive in the southeastern United States. I have seen no specimens from Panama but it could easily be adventive there. Suessenguth (in Rep. Spec. Nov. 39:4. 1935) reports a teratological specimen from Pearl Islands in San José in which the stamens are replaced by carpels.

7. ALTERNANTHERA WILLIAMSII (Standl.) Standl. in Jour. Wash. Acad. Sci. 15: 458. 1925.

Achyranthes williamsii Standl. in Contr. U. S. Nat. Herb. 18:89. 1916.

Erect or clambering pubescent perennials, the sparingly branched stems to 5 m. long. Leaves appressed pubescent, sometimes variegated with purple, ovate, apically acute to acuminate, basally rounded to acute, 2.5–10 cm. long, 1–4 cm. broad; petioles 2–8 mm. long. Inflorescences of terminal and axillary white to stramineous, globose to ovoid heads, 10–30 mm. long, 10–12 mm. broad, the usually unbranched peduncles 1–7 cm. long. Flowers perfect; bracts and bracteoles subequal, ovate, carinate, aristate, 2–4 mm. long; sepals 5, subequal, oblong, 3-ribbed and indurate basally, 4–6 mm. long, 1–1.5 mm. broad; stamens 5, united below into a tube, the pseudostaminodia lacerate and exceeding the anthers; ovary

globose; style 1, 1–2 times as long as the globose stigma. Fruit an indehiscent obovoid utricle, the seeds reddish brown, cochleate-orbicular, 1.2–1.5 mm. long.

CANAL ZONE: between Summit and Gamboa, *Greenman & Greenman 5244.* COLÓN: Ahorca Lagarto, *Cowell 255.* DARIÉN: vicinity Yape, Río Tuira, *Allen 4302*; Tucuti, Chepigana, *Terry & Terry 1388*; Cituro, *Williams 675.* PROVINCE UNKNOWN: *Sutton Hayes 949*; *Halsted in 1850.*

An inhabitant of dry thickets, this species ranges from Panama to southern Mexico. It is very closely related to the Mexican species *A. gracilis* (Mart. & Gal.) Standl. which supposedly differs in having globose heads, recurved sepals, trichotomous peduncles and black seeds. Intermediate forms do occur however. *A. williamsii* f. *purpurea* Standl., with purplish red leaves, is cultivated in the Canal Zone as an ornamental.

8. ALTERNANTHERA LAGUROIDES (Standl.) Standl. in Standl. & Cald. Lista Pl. Salvador 74. 1925.

Achyranthes laguroides Standl. in Contr. U. S. Nat. Herb. 18:90. 1916.

Erect or clambering pubescent perennials, the much branched stems to 4 m. long. Leaves densely sericeous, especially below, lanceolate to narrowly ovate, apically attenuate, basally attenuate, 2–10 cm. long, 1–3.5 cm. wide; petioles 1–4 mm. long. Inflorescences of terminal and axillary stramineous to whitish ovoid heads, 5–15 mm. long, 4–12 mm. broad, the peduncles to 9 cm. long, branched or unbranched, naked or leafy (when leafy, the heads may appear sessile). Flowers perfect; bracts and bracteoles subequal, ovate, acuminate to aristate, 2–3.5 mm. long; sepals 5, narrowly oblong, 1–3 nerved, scarcely indurate, 4–5.5 mm. long, with basal hairs almost exceeding the sepals; stamens 5, united below into a tube, the lacerate pseudostaminodia exceeding the anthers; ovary obovoid to globose; style 1, 2–3 times as long as the globose stigma. Fruit an obovoid utricle to 1 mm. long; mature seeds not seen.

According to Standley & Steyermark (in Field Mus. Bot. 24:149. 1946) this species ranges from Guatemala to Panama in dry thickets of the Pacific slope. In Guatemala it is called *botoncito.* Possibly Moquin was using this species in his description of *Telanthera pubiflora* α *monocephala,* the type of which was collected in Panama. I have not seen the type, but believe the description fits *A. laguroides* more closely than any of the other Central American species.

9. ALTERNANTHERA STENOPHYLLA (Standl.) Standl. in Field Mus. Bot. 8:9. 1930.

Achyranthes stenophylla Standl. in Contr. U. S. Nat. Herb. 18:90. 1916.

Ascending or erect sparsely strigose or glabrate perennials. Leaves sparsely pilose or glabrate, linear to linear-elliptic, apically acute, basally acuminate, 2.5–5 cm. long, 3–6 mm. broad; petioles 2–6 mm. long. Inflorescences of axillary and terminal stramineous cylindric heads, 6–10 mm. long, 5–6 mm. broad; peduncles unbranched, 2–5 cm. long. Flowers perfect, the bracts and bracteoles subequal, ovate, aristate, 1–2 mm. long; sepals 5, oblong, obscurely 3-nerved and indurate

basally, 2–2.5 mm. long; stamens 5, united below into a tube, the lacerate pseudostaminodia exceeding the anthers; ovary subglobose; style 1, 2–3 times as long as the globose stigma. Mature fruit not seen.

PROVINCE UNKNOWN: *Sutton Hayes 941.*

The type for this species was collected by Sutton Hayes in the year 1859-1860 and the only given locality was Panama. Apparently it is known only from the type collection. Except for the linear leaves, this species very strongly resembles the following species.

10. ALTERNANTHERA MEXICANA (Schlecht.) Hieron. Bot. Jahrb. 20: Beibl. 49:8. 1895.

Brandesia mexicana Schlecht. in Linnaea 7:392. 1832.
Telanthera microcephala Moq. in DC. Prodr. 13^2:371. 1849.
Telanthera mexicana Moq. loc. cit. 372. 1849.
Alternanthera lehmannii Hieron. in Bot. Jahrb. 20: Beibl. 49:8. 1895.
Achyranthes lehmannii (Hieron.) Standl. in Jour. Wash. Acad. 5:74. 1915.
Achyranthes mexicana (Schlecht.) Standl. loc. cit. 74. 1915.

Ascending or erect pilose or glabrate perennials, the scantily branched stems to 1 m. long. Leaves appressed pilose or glabrate, elliptic to ovate, apically attenuate, basally acute to cuneate, 2.5–10 cm. long, 1–5 cm. broad; petioles 2–15 mm. long. Inflorescences of axillary and terminal white to stramineous subglobose to cylindric heads, 5–10 mm. long, 4–7 mm. broad; peduncles mostly unbranched, to 9 cm. long. Flowers perfect, the bracts and bracteoles subequal, ovate, acuminate to aristate, 1–2 mm. long; sepals 5, oblong, obscurely 3-nerved and slightly indurate basally, 2–3.5 mm. long, 1 mm. broad; stamens 5, united below into a tube, the lacerate pseudostaminodia exceeding the filaments; ovary globose to obovoid; style 1, about twice as long as the globose stigma. Fruit an indehiscent obovoid utricle, 1–1.5 mm. long; seeds reddish brown, cochleate-orbiculate, about 1 mm. broad.

PROVINCE UNKNOWN: *Sutton Hayes 945.*

Inhabiting mesic forests, this species extends from Mexico south locally to Colombia. It is of more than casual interest that *Sutton Hayes 945* is *A. mexicana*, *Sutton Hayes 944* is the type of *A. panamensis* and *Sutton Hayes 941* is the type of *A. stenophylla*. The flowers of all these specimens are very similar indeed and would suggest that the latter two were mere vegetative variants of *A. mexicana*.

11. ALTERNANTHERA PANAMENSIS (Standl.) Standl. in Field Mus. Bot. 8:9. 1930.

Achyranthes panamensis Standl. in Contr. U. S. Nat. Herb. 18:89. 1916.

Erect or clambering pilose perennials, the stems much branched. Leaves appressed pilose, ovate to elliptic, apically acute to acuminate, basally subacute, 2–5.5 cm. long, 0.5–2 cm. wide; petioles 1–4 mm. long. Inflorescences of terminal and axillary stramineous to purplish globose to cylindric heads, 7–11 mm. long, about 7 mm. broad; peduncles mostly branched, 1–6 cm. long, villous.

Fig. 120. *Alternanthera panamensis* (habit and lower details) and *A. mexicana* (upper details)

Flowers perfect; bracts and bracteoles subequal, ovate, acuminate to aristate, 1–2 mm. long; sepals 5, oblong, strongly 3-nerved and indurate below, 2.5–3.5 mm. long; stamens 5, united below into a tube, the lacerate pseudostaminodia exceeding the filaments; ovary obovoid to subglobose; style 1, about as long as the globose stigma. Fruit an indehiscent subglobose utricle; seeds dark reddish brown to black, cochleate-orbiculate, 1 mm. broad.

PROVINCE UNKNOWN: *Sutton Hayes 944.*

This species, represented solely by the type collection, is perhaps just a casual variant of *A. mexicana* (Schlecht.) Hieron. It seems to bear the same relation to *A. mexicana* that the branched-pedunculate *A. gracilis* (Mart. & Gal.) Standl. bears to the unbranched-pedunculate *A. williamsii* (Standl.) Standl.

11. GOMPHRENA L.

GOMPHRENA L. Sp. Pl. 224. 1753.

Coluppa Adans. Fam. Fl. 2:268. 1763.
Bragantia Vand. Fasc. Pl. Nov. 6. 1771.
Wadapus Raf. Fl. Tell. 3:77. 1837.
Xerosiphon Turcz. in Bull. Soc. Nat. Mosc. 16:55. 1843.
Xeraea O. Ktze. Rev. Gen. 545. 1891.
Amarantoides Maza, Fl. Haban. 94. 1897.

Flowers perfect, bracteate and bibracteolate, sessile in spikes or heads. Sepals 5, basally connate or discrete, hypogynous, concave, subequal, colorless or brightly colored. Stamens 5, hypogynous, the filaments connate forming a deep stamen tube, the anthers sessile at the summit of the tube; pseudostaminodia 2-lobate; anthers 2-locellate, introrse, medially attached. Ovary globose to obovoid, 1-locular, 1-ovulate, the ovule campylotropous on an elongate flattened funicle; style 1, filiform, about as long as the 2 filiform stigmata. Fruit an indehiscent utricle; seeds cochleate-orbiculate. Pubescent erect or decumbent annual or perennial herbs. Leaves opposite, sessile or petiolate, entire, usually pubescent, apparently deciduous. Inflorescences of terminal and occasionally axillary globose to cylindric solitary or clustered heads, usually subtended by foliar leaves.

This genus of nearly a hundred species, with some native to tropical America and others to tropical Austral-Asia, seem to reach its best development in South America. Several species are widely cultivated, as is the "bachelor's button", *G. globosa,* a rather handsome ornamental with edible leaves. Four species are known from Central America but only two are reported from Panama.

a. Heads 5–14 mm. in diameter; bracteoles 4–6 mm. long; leaves 1–5 cm. long..... 1. G. DECUMBENS
aa. Heads 15–25 mm. in diameter; bracteoles 7–12 mm. long; leaves 2–10 cm. long..... 2. G. GLOBOSA

1. GOMPHRENA DECUMBENS Jacq. Hort. Schoenbr. 4:41. 1804.

Xeraea decumbens O. Ktze. Rev. Gen. 545. 1891.
Gomphrena decumbens f. *albiflora* Chod. & Hassl. in Bull. Herb. Boiss. 2^3:389. 1903.
Gomphrena decumbens f. *roseiflora* Chod. & Hassl. loc. cit. 389. 1903.

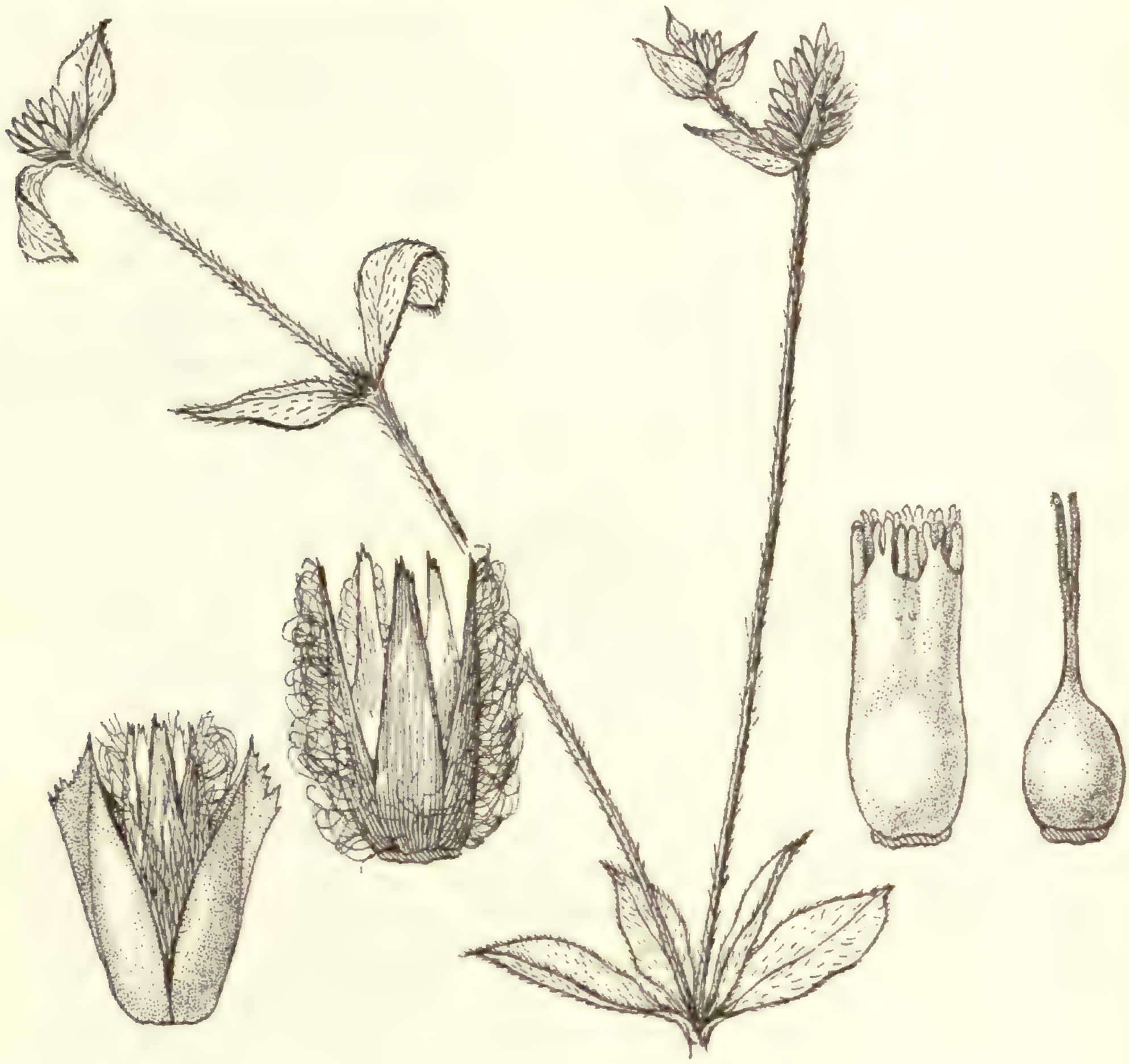

Fig. 121. *Gomphrena decumbens*

Gomphrena ixiamensis Rusby, in Bull. N. Y. Bot. Gard. 6:502. 1910.
Gomphrena decumbens var. *genuina* Stuchlík, in Rep. Spec. Nov. 11:156. 1912.
Gomphrena decumbens var. *grandifolia* Stuchlík, loc. cit. 157. 1912.
Gomphrena perennis subsp. *pseudodecumbens* Stuchlík, loc. cit. 153. 1912.
Gomphrena perennis f. *simplex* Stuchlík, loc. cit. 153. 1912.
Gomphrena dispersa Standl. in Contr. U. S. Nat. Herb. 18:91. 1916.
Gomphrena decumbens var. *carinata* Suesseng. in Rep. Sp. Nov. 39:8. 1935.

Prostrate or decumbent pilose annual or perennial herbs, the much branching stems to 50 cm. long, often rooting at the nodes and forming mats. Leaves sericeous to strigose, occasionally glabrate, oblong to ovate or obovate, apically acute to rounded and mucronate, basally acute to attenuate, 1–5 cm. long, 0.5–2.5 cm. broad; petioles 1–5 mm. long. Inflorescences of terminal and axillary ovoid to cylindric whitish or purplish heads, occasionally clustered, 4–20 mm. long, 5–14 mm. broad, subtended by ovate leaves 0.5–2 cm. long. Flowers perfect; bracts

persistent, ovate, acuminate, 1.5–3 mm. long; bracteoles narrowly to broadly cristate, equaling or exceeding the sepals, 4–6 mm. long; sepals 5, subequal, basally connate, cinereous- to rufous-lanate, ultimately indurate and closely embracing the fruit; stamens 5, subequal, the anthers sessile between the 5 2-lobate pseudostaminodia; stamen tube 3–6 mm. long; ovary globose; style 1, 1–1.5 mm. long; stigmata 2, 1–1.5 mm. long. Fruit an indehiscent areolate utricle 1–2 mm. long; seeds cochleate-orbiculate, yellowish to reddish brown, ocellate, 1.5–1.7 mm. broad.

BOCAS DEL TORO: Research grounds, region of Almirante, *Cooper 138*. CANAL ZONE: open sunny area next to road, Corrosion Laboratory, vicinity of Miraflores Locks, *Stern, Chambers et al. 68*; Ancón, *Greenman & Greenman 5015*; vicinity of Miraflores Lake, *White & White 192*; Pedro Miguel, *Bro. Heriberto 19*. CHIRIQUÍ: vicinity of Puerto Armuelles, 0–75 m., *Woodson & Schery 819*.

This species ranges from the West Indies and Mexico to Panama and from Brazil and Bolivia to Argentina. Common names in Guatemala are *botoncillo, sangrinaria, sanguinaria, siempreviva* and *siempreviva de monte*; other names in the Yucatan and adjoining regions are *chacmol, tmuul, amor seco* and *secicante*. Standley (in Contr. U. S. Nat. Herb. 18:91. 1916) has separated a variant, with the crests of the bracteoles conspicuously widest at the apex, as *G. dispersa*, which seems to occur throughout the range of *G. decumbens*. No correlated differences exist and transitions occur, so *G. dispersa* is reduced to synonymy. As Suessenguth (in Rep. Spec. Nov. 39:8. 1935) has noted *Greenman & Greenman 5015* is intermediate between *G. decumbens* and *G. nitida* Rothr., a questionably distinct species supposed to differ in having lacinate-dentate crests, larger rarely purple heads and an erect habit. *Palmer 401* from Mexico has crests both dentate and laciniate-dentate, or even absent; the specimen also has both included and exserted stamen tubes. This particularly illuminating example serves to demonstrate that *G. nitida* is hardly more deserving of specific status than is *G. dispersa*.

2. GOMPHRENA GLOBOSA L. Sp. Pl. 224. 1753.

Gomphrena globosa β carnea Moq. in DC. Prodr. 13²:409. 1849.
Gomphrena globosa γ albiflora Moq. loc. cit. 409. 1849.
Xeraea globosa O. Ktze. Rev. Gen. 545. 1891.
Amarantoides globosus Maza, Fl. Haban. 94. 1897.
Amarantoides globosus albiflorus Maza, loc. cit. 95. 1897.
Gomphrena globosa var. *aureiflora* Stuchlík, in Rep. Spec. Nov. 12:340. 1913.

Erect or ascending pilose annual herbs, the branching stems to 60 cm. high. Leaves sericeous, occasionally glabrate, oblong to ovate or obovate, apically acute and mucronate, basally rounded to attenuate, 2–10 cm. long, 0.5–5 cm. broad; petioles 1–15 mm. long. Inflorescences of terminal and axillary reniform to cylindric variously colored heads or spikes, occasionally clustered, 10–25 mm. long, 15–25 mm. broad, subtended by ovate leaves 5–20 mm. long. Flowers perfect; bracts persistent, ovate, acuminate, 3–4 mm. long; bracteoles dentate-cristate, exceeding the sepals, 7–12 mm. long, 2–3.5 mm. broad; sepals 5, subequal, basally connate, cinereous- to rufous-lanate, ultimately indurate and closely embracing the fruit, 5–6.5 mm. long; stamens 5, the anthers sessile between the 5 2-lobate

pseudostaminodia; stamen tube 4–8 mm. long; ovary globose; style 1, 1–1.5 mm. long; stigmata 2, 1–1.5 mm. long. Fruit an indehiscent areolate utricle 1.5–2.5 mm. long; seeds cochleate-orbiculate, reddish brown, ocellate, 1.5–2 mm. broad.

Cultivated and escaped in many regions of the world, this species may be a native of America although it was originally described from India. Standley (in Contr. U. S. Nat. Herb. 27:173. 1928) reports that it occurs in Panama as a cultivant and an escape. In Panama it is called *siempreviva* and *suspiro*. The names *amor seco*, *inmortal* and *botón* are also used in Guatemala. Some of these vernacular names suggest the persistence of the flowerss which makes them popular in wreaths and dry floral arrangements. That the differences between this and the preceding species are quantitative may suggest a polyploid derivation.

NYCTAGINACEAE*

Herbs, shrubs, or trees, sometimes scandent, the stems frequently swollen at the nodes, particularly in the herbaceous genera, and sometimes armed with axillary spines. Leaves alternate, opposite, whorled, or approximate, simple, estipulate, entire. Flowers monochlamydeous, perfect or unisexual, in various cymose inflorescences, occasionally solitary, the bracteoles often enlarged and involucrate, herbaceous or petalaceous and enclosing one or more flowers. Perianth monochlamydeous, herbaceous or petalaceous, tubular to infundibuliform, campanulate, urceolate, or salverform, involute-plicate in aestivation, the base of the tube persistent in fruit, the limb persistent or deciduous. Stamens 1 to many, hypogynous, the filaments unequal, usually united at the base, the anthers included or exserted, dorsifixed near the base. Ovary 1-celled, containing a solitary basal ovule; style elongate, short, or lacking. Fruit a fleshy, coriaceous, or woody anthocarp, occasionally bearing viscid stipitate glands.

Nyctaginaceae are an essentially tropical and subtropical family, particularly in the New World. The Four-o'clock Family is represented in Panama by five indigenous genera, but more familiar to the general public are the introduced genera *Bougainvillea* and *Mirabilis*. *Bougainvillea*, almost ubiquitously planted as an ornamental woody vine because of its handsome clusters of three showy magenta, red, pink, white, or yellow bracts subtending the inconspicuous flowers, is a South American genus which does not appear to naturalize readily in Panama. The plants variously are referred to *B. glabra* Choisy and *B. spectabilis* Willd. It usually is known by its Latin name, or by the vernacular *veranera* and *flor de verano* because of its habit of blooming in the dry season. *Mirabilis jalapa* L., the common four-o'clock of the English, is a herb with showy red, white, yellow, or variegated flowers set in individual green calyx-like involucres. It is cultivated in gardens and escapes as a vigorous weed in waste ground and roadsides. It is known locally as *maravilla* and *buenas tardes* because of its vespertine blooms.

The taxonomy of the Nyctaginaceae, particularly of the woody dioecious genera, is very confused. It seems entirely possible that interspecific hybridization may be one factor responsible for obscuring the lines of the species. The species bibliographies which follow are frankly provisional; to some, additional synonyms will have to be added from the South American literature and some such names possibly will have to take precedence over the Central American which are adopted here. The detailed study essential to a competent treatment unfortunately is beyond the scope of this flora.

A. Herbs; flowers bisexual..... 1. BOERHAVIA

AA. Trees, shrubs, and woody lianas; flowers unisexual, dioecious.

B. Staminate flowers with deeply included stamens; pistillate flowers with the ovary sessile and free from the staminodes; bracteoles borne immediately beneath the perianths; plants unarmed.

C. Stamens 25–30; staminate perianths broadly campanulate; anthocarps woody, not glandular, the perianth limb persistent. 2. CEPHALOTOMANDRA

*With the collaboration of Harold J. Kidd.

CC. Stamens 5–10, usually 8; staminate perianths tubular to urceolate; anthocarps fleshy, the perianth limb withering and at length abscissing..... 3. NEEA

BB. Staminate flowers campanulate, with widely exserted stamens; pistillate flowers with the ovary stipitate.

C. Plants unarmed; anthocarps fleshy, not glandular, the perianth limb persistent; bracteoles borne immediately beneath the perianths; pistillate flowers with the staminodes about as long as the ovary and bearing conspicuous sterile anthers..... 4. GUAPIRA

CC. Plants usually armed with stout axillary spines; anthocarps coriaceous, armed with conspicuous stipitate glands; bracteoles not borne immediately beneath the perianths; pistillate flowers with the staminodes reduced to a low, occasionally minutely glandular-dentate disc..... 5. PISONIA

1. BOERHAVIA L.

BOERHAVIA L. Sp. Pl. 3. 1753.

Boheravia Parodi, in Anal. Soc. Cient. Argent. 5:210. 1878.
Boerhaavia auct.

Annual or perennial herbs. Leaves opposite or subopposite, petiolate, frequently unequal at the nodes, the blade undulate or sinuate, conspicuously raphidulous. Inflorescence terminal, paniculiform to racemiform, many-flowered. Flowers small, perfect, subtended by 1–3 minute bracteoles, the perianth tube persistent, more or less herbaceous, frequently glandular, the perianth limb deciduous, petalaceous, obscurely 5-lobed; stamens 1–5, included or exserted; ovary shortly stipitate, the stigma capitate, more or less exserted. Anthocarp obpyramidal to obovoid or subellipsoid, glabrous to glandular, 3- to 5-angulate.

Numerous species in the tropics and subtropics of both hemispheres. Both species in Panama are weeds and possibly not indigenous.

a. Annuals; stems erect or ascending, glabrous or essentially so; leaves reddish-punctate beneath; inflorescences not leafy, the flowers in 2- to 3-flowered dichasia, distinctly pedicellate; anthocarps obpyramidal, truncate, glabrous, conspicuously pedicellate..... 1. B. ERECTA

aa. Perennials; stems decumbent, more or less glabrous; leaves not punctate beneath; inflorescences leafy-bracted, the flowers in small glomerulate clusters, sessile or subsessile; anthocarps obovoid to subellipsoid, obtuse or somewhat beaked, glandular, sessile or subsessile..... 2. B. DIFFUSA

1. BOERHAVIA ERECTA L. Sp. 3. 1753.

Boerhavia elongata Salisb. Prodr. 56. 1796.
Boerhaavia virgata HBK. Nov. Gen. 2:215. 1817.
Boerhaavia discolor HBK. loc. cit. 1817.
Boerhaavia atomaria Raf. Aut. Bot. 40. 1840.
Valeriana latifolia Mart. & Gal. in Bull. Acad. Brux. 11^1:124. 1844.
Boerhaavia paniculata β subacuta Choisy, in DC. Prodr. 13^2:451. 1849.
Boerhavia thornberi M. E. Jones, Contr. West. Bot. 12:72. 1908.
Boerhaavia erecta thornberi (M. E. Jones) Standl. in Contr. U. S. Nat. Herb. 12:381. 1909.

Annual herbs; stems erect or ascending, 2–8 dm. tall, rather slender, glabrous or essentially so. Leaves opposite or subopposite, often unequal at the nodes, petiolate; blade rather irregularly ovate-rhombic, obtuse to rounded, or infrequently

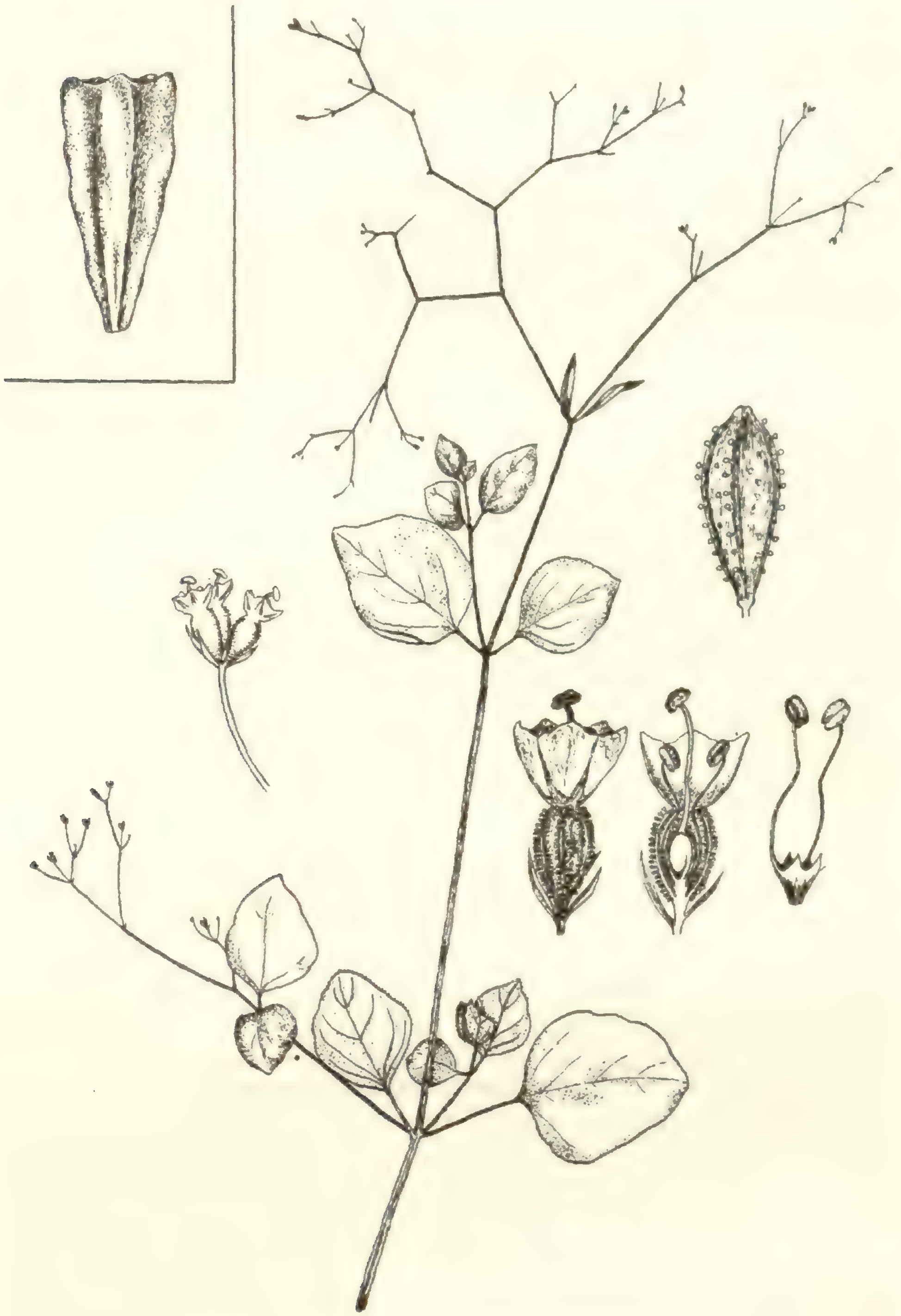

Fig. 122. *Boerhavia diffusa*; insert: fruit of *B. erecta*

acute, at the apex, broadly obtuse to rounded at the base, undulate or sinuate, 2–9 cm. long, 1–4 cm. broad, glabrous or essentially so, yellowish green above, paler and more or less conspicuously bracteate, glabrous or essentially so. Flowers in pedunculate 2- to 3-flowered dichasia, distinctly pedicellate, the perianth tube 1.0–1.5 mm. long, about 0.5 mm. broad, herbaceous, glabrous, the perianth limb campanulate, about 0.5–0.7 mm. long, white or pink; stamens 2–3, slightly exserted. Anthocarps obpyramidal, truncate, glabrous, 3–4 mm. long, 1.0–1.5 mm. broad, borne upon accrescent pedicels of about equal length.

A small weed of beaches, open thickets, fields, roadsides, and wasteland; southern United States, Antilles, Central and South America; a rare sporadic ruderal in tropical Africa.

CANAL ZONE: Gamboa, *Bro. Heriberto 28, Standley 28461*; Monte Lirio, *Maxon 6860*; Obispo, *Standley 31775*; Gatún, *Cowell 296*; Frijoles, *Piper 5829*; New Frijoles, *Pittier 6836*; Balboa, *Bro. Celestine 10*; Paraíso, *Pittier 2529*; Summit, *Standley 30133*; Monkey Hill, *Cowell 28*. CHIRIQUÍ: Puerto Armuelles, *Woodson & Schery 838*. COLÓN: Colón, *Macbride & Featherstone 1, Piper 5892, Rose 22084*.

The glabrous anthocarps and inflorescences of *B. erecta* have made this species less widely dispersed as a ruderal than *B. diffusa*.

2. BOERHAVIA DIFFUSA L. Sp. Pl. 3. 1753.

Boerhaavia coccinea Mill. Gard. Dict. ed. 8. Boerhaavia no. 4. 1768.
Boerhavia caribaea Jacq. Obs. Bot. 4:5. *tab. 84*. 1771.
Boerhavia diandra Aubl. Hist. Pl. Guian. 1:4. 1775.
Boerhaavia paniculata A. Rich. Act. Soc. Hist. Nat. Paris 1:105. 1792.
Boerhaavia polymorpha A. Rich. loc. cit. 185. 1792.
Boerhavia hirsuta Willd. Phytog. 1:1. 1794.
Boerhaavia adscendens Willd. Sp. Pl. 1:19. 1798.
Boerhaavia viscosa Lag. & Rodr. in Anal. Ci. Nat. 4:256. 1801.
Boerhaavia decumbens Vahl, Enum. Pl. 1:284. 1805.
Boerhaavia laxa Pers. Syn. Pl. 1:36. 1805.
Boerhavia squamata Raf. Aut. Bot. 40. 1840.
Boerhaavia sonorae Rose, in Contr. U. S. Nat. Herb. 1:111. 1891.
Boerhaavia diffusa var. *hirsuta* (Jacq.) O. Ktze. Rev. Gen. 533. 1891.
Boerhaavia diffusa var. *paniculata* (Rich.) O. Ktze. loc. cit. 1891.
Boerhaavia diffusa var. *viscosa* (Lag. & Rodr.) Heimerl, Beitr. Syst. Nyct. 27. 1897.
Boerhaavia viscosa forma *oligadena* Heimerl, in Ann. Cons. Jard. Genève 5:189. 1901.
Boerhavia ramulosa M. E. Jones, Contr. West. Bot. 10:40. 1902.
Boerhaavia viscosa apiculata Standley, in Contr. U. S. Nat. Herb. 12:383. 1909.
Boerhaavia ixodes Standley, loc. cit. 13:423. 1911.
Boerhaavia coccinea forma *parcehirsuta* Heimerl, in Urb. Symb. Ant. 7:212. 1912.

Perennial herbs; stems decumbent to ascending, 4–12 dm. long, rather slender, more or less viscid-puberulent. Leaves opposite or subopposite, often unequal at the nodes, petiolate; blade orbicular to rhombic-ovate below, frequently grading to lanceolate above, obtuse to rounded or acute at the apex, obtuse to rounded at the base, undulate or sinuate, 2–6 cm. long, 2–5 cm. broad, more or less puberulent to glabrate, yellowish green above, paler beneath, not punctate; petiole 1–4 cm. long. Inflorescences paniculiform, lax and many-flowered, leafy-bracteate at least below, viscid-puberulent to glabrate. Flowers in pedunculate glomerulate clusters, sessile or subsessile, the perianth tube 0.7–1.0 mm. long, somewhat less than 0.5

mm. broad, herbaceous, minutely glandular, the perianth limb campanulate, about 0.5 mm. long, red to purple, rarely white; stamens 3, slightly exserted. Anthocarps obovoid to subellipsoid, obtuse to obscurely beaked, 3–4 mm. long, 1 mm. broad, glandular, sessile or subsessile.

A weed widely dispersed throughout the tropics and subtropics of America, Africa, Asia, and Oceania. *Carasola* (Taboga Isl.).

BOCAS DEL TORO: Lincoln Creek, Chaguinola valley, *Dunlap 377*. CANAL ZONE: Frijoles, *Wilson 51*; Empire, *Hunter & Allen 786*; Ancón, *Greenman & Greenman 5042*; between Corozal and Ancón, *Pittier 2188*; Ahorca Lagarto to Culebra, *Cowell 369*; Balboa, *Macbride & Featherstone 39*; Monte Lirio, *Maxon 6847*; Gamboa, *Bro. Heriberto 29, Standley 28344, Piper 5649*; Gatún, *Standley 27321*; Darién, *Standley 31520, Macbride 2684*. CHIRIQUÍ: Puerto Armuelles, *Woodson & Schery 820*. PANAMÁ: Taboga Island, *Pittier 3534, Killip 3177, Allen 101, Standley 27114, 27845*; San José Island, Pearl Archipelago, *Harlow 47*. SAN BLAS: Permé, *Cooper 222*.

Boerhavia erecta and *B. diffusa* frequently grow together, and hybridization must occur occasionally but insufficiently to blur the outline of the species. In Standley's treatments of *Boerhavia* for the North American Flora and the Flora of the Panama Canal Zone, the parental species would be called *B. erecta* and *B. caribaea*, respectively, and the putative hybrids *B. coccinea*. Such plants will usually key readily to *B. diffusa* in the present treatment. A rather extensive examination of herbarium specimens has revealed no tangible differences between *B. caribaea* and *B. coccinea* of the New World and *B. diffusa* of the Old World. The species appears plainly to be an effusive pantropic weed, the dispersal of which has been greatly facilitated by the viscid anthocarps. It is probably, but not certainly, of American origin.

2. CEPHALOTOMANDRA Karst. & Triana

CEPHALOTOMANDRA Karst. & Triana, ex Karst. in Linnaea 28:429. 1856.

Dioecious trees. Leaves opposite to irregularly approximate. Inflorescences terminal, corymbosely thyrsiform. Flowers small, immediately subtended by 1–3 minute bracteoles. Staminate flowers broadly campanulate; stamens 25–30, unequal, included, the short tube of the filaments hypogynous and free from the sessile pistillode. Pistillate flowers unknown. Anthocarps woody, eglandular, longitudinally costate, the limb of the perianth persistent.

A single species, Panama (?) and Colombia.

1. CEPHALOTOMANDRA FRAGRANS Karst. & Triana, ex Karst. in Linnaea 28:429. 1856.

Cephalotomandra panamensis Standl. in North Am. Flora 21:179. 1918.

Dioecious trees to 25 m. tall. Branches rather stout, glabrous, with a longitudinally striate, scarcely lenticellate, yellow periderm. Leaves rather sparse, long-petiolate, the blade broadly elliptic to ovate-elliptic, Obtusely acuminate to acute, base obtuse or rounded, 8–25 cm. long, 2.5–15.0 cm. broad, glabrous, firmly membranaceous or subcoriaceous, yellowish green, venation prominent but rather

Fig. 123. *Cephalotomandra fragrans*

distant; petiole 1–12 cm. long. Inflorescence 10–20 cm. long, long-pedunculate, many-flowered, minutely puberulent, the ultimate cymules typically dichasial with the terminal flower sessile and 1-bracteolate and the lateral definitely pedicellate and 3-bracteolate. Staminate perianth broadly campanulate, yellowish, about 4 mm. long and 3 mm. broad at the conspicuously inflated, slightly spreading limb, minutely puberulent-papillate. Anthocarps oblong-fusiform, crowned by the persistent perianth limb, about 1 cm. long and 3 mm. broad, glabrous.

CANAL ZONE (?): locality unknown, *Sutton Hayes 998*.

The holotype of *C. panamensis*, cited above from the herbarium of the New York Botanical Garden, is suspiciously similar in all essential details to an isotype

of *C. fragrans* (*Triana 998*) deposited in the herbarium of the Missouri Botanical Garden and originally distributed by the British Museum. It may be merely a peculiar coincidence, but it seems more than strange that both sheets bear a small fruiting twig and a small twig with a staminate inflorescence in identical stages of development, and that both the Triana specimen and that ascribed to Sutton Hayes bear the collection number *998*. Karsten's description of *Cephalotomandra* is extremely vague in details of the pistillate inflorescence, and the account of the genus in Bentham & Hooker's Genera Plantarum, although describing the fruit and the staminate flowers, expressly states that the pistillate flowers were not seen by them. I think that it is altogether probable that the New York sheet is actually a second duplicate of Triana's original collection of *C. fragrans* and that its ascription to Sutton Hayes is in error. It is doubtful, therefore, that the genus *Cephalotomandra* can be included in the flora of Panama without serious question.

3. NEEA R. & P.

NEEA R. & P. Fl. Per. Prodr. 52. 1794.

Neeania Raf. Princ. Som. 30. 1814.
Mitscherlichia Kunth, in Abh. Berl. Akad. 1831:209. 1831.
Eggersia Hook. f. in Hook. Ic. 15:1. *t. 1401*. 1883.

Dioecious trees and shrubs. Leaves opposite to irregularly approximate. Inflorescences terminal, thyrsiform. Flowers small, immediately subtended by 1–3 minute bracteoles. Staminate flowers urceolate; stamens 5–10, usually 8, unequal, included, the short tube of the filaments surrounding the sessile pistillode. Pistillate flowers urceolate or tubular-urceolate, the limb of the perianth erect or spreading, the staminodes usually somewhat surpassing the ovary and with enlarged sterile anthers, the pistil sessile. Anthocarps fleshy, eglandular, the limb of the perianth withering and at length abscissing.

Numerous species in the Antilles, and Central and South America; southern peninsular Florida.

a. Cymules strikingly dichasial, the terminal flowers sessile, the lateral with relatively long slender pedicels; leaves predominantly rather small or of moderate size, and only very rarely somewhat pubescent beneath.
  b. Inflorescences usually quite glabrous, the pedicels of lateral flowers as long as the perianths or somewhat longer; staminate perianths ovoid-urceolate; anthocarps broadly ellipsoid ..... 1. N. DELICATULA
  bb. Inflorescences minutely puberulent, the pedicels as long as the perianths or somewhat shorter; staminate perianths oblong-urceolate; anthocarps narrowly ellipsoid ..... 2. N. LAETEVIRENS
aa. Cymules obscurely dichasial, both terminal and lateral flowers subsessile or with similar short stout pedicels; leaves predominantly large and frequently more or less pubescent beneath ..... 3. N. AMPLIFOLIA

1. NEEA DELICATULA Standl. in Contr. U. S. Nat. Herb. 18:98. 1916.

Torrubia panamensis Standl. in North Am. Fl. 21:185. 1918.

Dioecious shrubs or small trees to 6 m. tall. Branches rather slender, glabrous or minutely puberulent when very young, inconspicuously lenticellate at maturity.

Leaves petiolate, the blade predominantly obovate to obovate-elliptic, acuminate, obtusely cuneate at the base, 4–12 cm. long, 2–4 cm. broad, firmly membranaceous, glabrous, the petiole 2–15 mm. long. Inflorescences 4–7 cm. long, usually glabrous, rarely minutely puberulent, rather few-flowered, the peduncles slender, the cymules strikingly dichasial, the terminal flowers sessile, the lateral with slender pedicels as long as the flowers or somewhat longer. Staminate perianths ovoid-urceolate, about 6 mm. long and 3 mm. broad, glabrous. Pistillate perianths tubular, about 3 mm. long and somewhat less than 1 mm. broad, minutely puberulent to glabrous. Anthocarps broadly ellipsoid or ellipsoid-obovoid, 8–10 mm. long, 4–5 mm. broad, pink or red.

Panama, in forests and thickets near sea level to 100 m. alt.

CANAL ZONE: Balboa, *Standley 32114*. PANAMÁ: around Alajuela, Chagres valley, *Pittier 3472*; Tumba Muerto Road, near Panamá, *Standley 29805*; near Matías Hernández, *Standley 28880*; Río Tapía, *Standley 28201*; Taboga Island, *Pittier 3602*; Trapiche Island, Perlas Islands, *Allen 2422*. PROVINCE UNKNOWN: *Seemann s. n. pro parte*.

I believe it quite possible that *N. delicatula* and *N. anisophylla* Ernst, of Colombia and Venezuela (= *N. wiesneri* Heimerl) may be conspecific. The leaves of the latter, however, appear to be somewhat larger than those of the former, as well as of a somewhat different pattern of shape; the staminate perianths, also, seem to be somewhat narrower than those from Panama.

The type specimen of *Torrubia panamensis* definitely is *Neea* and differs from the other specimens cited only in the thin minute pubescence of the peduncles.

Comments on the Seemann collection are included in the discussion of *Guapira standleyana*. Seemann's illustration of *Pisonia pacurero* (in Bot. Voy. Herald, *pl. 34*. 1854) may have been prepared from a specimen of *Neea delicatula*, but is not definitely diagnostic.

2. NEEA LAETEVIRENS Standl. in Field Mus. Publ. Bot. 4:204. 1929.

Neea xanthina Standl. in Ann. Missouri Bot. Gard. 30:86. 1943.
Neea psychotrioides auct. pro parte, non Donn. Sm.

Dioecious shrubs or small trees to 7 m. tall. Branches rather slender, minutely puberulent to glabrate, inconspicuously lenticellate at maturity. Leaves petiolate, the blade elliptic to obovate- or oblong-elliptic, rarely lanceolate, acuminate, obtuse to cuneate, 5–23 cm. long, 3–9 cm. broad, glabrous or rarely very inconspicuously puberulent beneath particularly on the midrib, the petiole 0.5–4.0 cm. long. Inflorescences 8–20 cm. long, minutely puberulent, many-flowered, the cymules strikingly dichasial with the terminal flowers sessile and the lateral with slender pedicels as long as the flowers or somewhat shorter. Staminate flowers oblong-urceolate, 6–9 mm. long, 2–3 mm. broad, thinly and minutely puberulent, white, yellow, or red. Pistillate flowers tubular, the lobes erect or suberect, conspicuously thickened at the orifice of the tube, 4–5 mm. long, 1.0–1.5 mm. broad, densely and minutely puberulent. Anthocarps narrowly ellipsoid, 7–10 mm. long, 2–3 mm. broad, red.

Panama and Costa Rica, in moist forests and thickets near sea level.

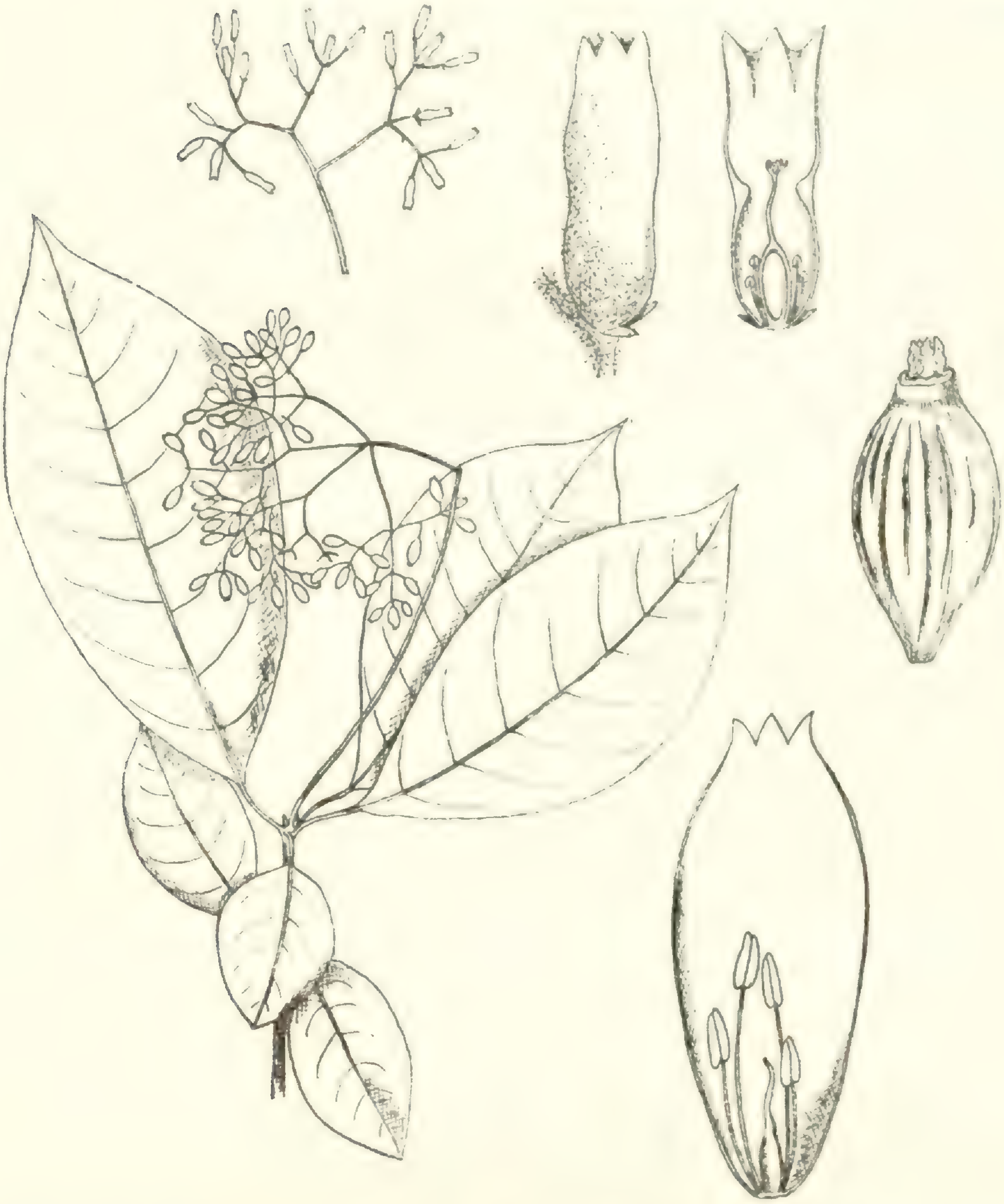

Fig. 124. *Neea laetevirens*

BOCAS DEL TORO: Old Bank Island, *Von Wedel 1885, 1970*; Little Bocas, *Von Wedel 2533*; Fish Creek Hills, *Von Wedel 2433*; Shepherd Island, *Von Wedel 2695*; Río Caricamola, *Woodson, Allen & Seibert 1914*; region of Almirante, *Cooper 340, 544, 572a*; Isla Colón, *Von Wedel 2793, 2842*; Water Valley, *Von Wedel 730, 979, 1678, 1810*; Changuinola Valley, *Dunlap 94, 136, 511, 519, 562, 488, 329*; *Cooper & Slater 106*; Farm Six, *Stork 94*; vicinity of Chiriquí Lagoon, *Hart 168*; *Von Wedel 1105, 1182, 1298, 1145*. SAN BLAS: Permé, *Cooper 639*.

This is the species which has been determined almost invariably as *Neea psychotrioides* in Panama. The specimens enumerated above are relatively uniform; but the species apparently is capable of hybridization with *N. amplifolia*, although such

specimens will usually key to the latter under the discussion of which they will be noted.

There probably are scarcely more than a half dozen valid species of *Neea* in Central America. These seem to form two vicarious series upon the Pacific and the Atlantic slopes, recognizable by the staminate perianths which are ovoid- or oblongoid-urceolate respectively. True *N. psychotrioides* is a representative of the former series, as is *N. delicatula* of Panama. Both Panamanian species are distinguishable from their related species to the north by their longer-pedicelled flowers and proportionally longer lobes of the pistillate perianths. True *N. psychotrioides* extends on the Pacific slope from southern Mexico to Nicaragua and is not yet known to occur in Costa Rica, although it might be expected in Guanacaste.

In Costa Rica, *N. laetevirens* has been collected at Puerto Limón, and up the Reventazón and Parismina watersheds to the highlands of the provinces of Alajuela and Cartago.

3. Neea amplifolia Donn. Sm. in Bot. Gaz. 61:386. 1916.

Neea pittieri Standl. in Contr. U. S. Nat. Herb. 13:383. 1911.
Neea orosiana Standl. in Journ. Wash. Acad. Sci. 15:473. 1925.
Neea urophylla Standl. in Field Mus. Publ. Bot. 4:203. 1929.
Neea pycnantha Standl. in Ann. Missouri Bot. Gard. 30:85. 1943.
Neea psychotrioides auct. pro parte, non Donn. Sm.

Dioecious shrubs and small trees to about 7 m. tall. Branches moderately stout, densely ferruginous-pubescent to glabrate. Leaves petiolate, the blade ovate- to obovate-elliptic, usually more or less caudate-acuminate, obtuse to cuneate at the base, 7–36 cm. long, 3–15 cm. broad, firmly membranaceous, glabrous above but frequently more or less puberulent beneath, the petiole 0.5–5.0 cm. long. Inflorescences 4–15 cm. long, essentially glabrous to densely ferruginous-pubescent, rather few-flowered to many-flowered and occasionally greatly proliferous and the flowers and bracts becoming phylloid; cymules obscurely dichasial, both terminal and lateral flowers subsessile or with essentially similar short stout pedicels. Staminate perianths tubular-urceolate, 5–10 mm. long, 2–3 mm. broad, essentially glabrous to minutely puberulent to essentially glabrous. Anthocarps ellipsoid to ovoid, 7–12 mm. long, glabrous to minutely puberulent, red.

Panama and Costa Rica, in forests and moist thickets, from near sea level to about 700 m.

Bocas del Toro: region of Almirante, Daytonia Farm, *Cooper 545, 373*; Almirante region, *Cooper & Slater 58*; Changuinola valley, *Cooper & Slater 60, 140*; Cricamola, *Cooper 491*; Fish Creek Mts., *Von Wedel 2267*; vicinity of Chiriquí Lagoon, *Von Wedel 1011, 1017*; Water Valley, *Von Wedel 1574, 1609, 1503, 1433, 927*. Canal Zone: hills north of Frijoles, *Standley 27427, 27509*; Margarita Swamp, south of France Field, *Maxon & Valentine 7048*; Gatún, *Sutton Hayes 626*; railroad relocation between Gorgona and Gatún, *Pittier 2265, 2271*; Barro Colorado Island, *Frost 123, Kenoyer 491, 638, Aviles 30, Bailey & Bailey 120, 522, Wetmore & Abbe 22, Standley 31310, 31336, 40905, 40955, 41023, 41015*. Chiriquí: Progreso, *Cooper & Slater 184*. Coclé: region north of El Valle de Antón, *Allen 3732*. Colón: between France Field and Catival, *Standley 30182*; along Río Fató, *Pittier 3912*. Darién: trail between Pinogana and Yavisa, *Allen 268*; forests around Pinogana, *Pittier 6547*. San Blas: forests around Puerto Obaldía, *Pittier 4397*.

Neea amplifolia usually can be keyed without difficulty from the two preceding species, particularly by means of the inflorescence characters, the predominantly larger leaves and staminate perianths, and the more frequent and abundant indument. In all respects intermediates occur, nevertheless, and the relative abundance of disparate specimens, particularly from Bocas del Toro, where *N. laetevirens* also is abundant and variable, provides grounds for strongly suspected hybridization.

The proliferation and phyllody of the inflorescence is a frequent and puzzling propensity of this species, the agent of which is obscure. In addition, both in *N. amplifolia* and in *N. laetevirens*, the terminal staminate flowers occasionally develop at the expense of the lateral.

4. GUAPIRA Aubl.

GUAPIRA Aubl. Hist. Pl. Guian. 1:308; 3: *t. 119.* 1775.

Gynastrum Neck. Elem. 1:224. 1790.
Torrubia Vell. Fl. Flum. 139. 1825; Icon. 3: *t. 150.* 1827, *non* Tul.

Dioecious trees and shrubs. Leaves opposite to irregularly approximate. Inflorescences terminal, frequently at the tips of short lateral branches, corymbosely thyrsiform. Flowers small, immediately subtended by 1–3 minute bracteoles. Staminate flowers campanulate; stamens usually 6–8, unequal, widely exserted, the short tube of the filaments adnate to the stipe of the pistillode. Pistillate flowers tubular to tubular-campanulate, the limb of the perianth erect or spreading, the staminodes about as long as the ovary and with enlarged sterile anthers, the short tube of the filaments adnate to the stipe of the pistil. Anthocarps fleshy, eglandular, the limb of the perianth persistent and rather fleshy.

Numerous species in the Antilles, and Central and South America.

There can be little doubt that *Guapira* Aubl. is congeneric with *Torrubia* Vell. as suggested by Heimerl (in Engl. Nat. Pflanzenfam. ed. 2. 16^c:127. 1934) and not an indecipherable verbenacea as previously held by many (although questioned by Bentham & Hooker). The specimen illustrated by Aublet obviously is pistillate and, with the understandable error of the four to five minute "leaflets of the calyx [i. e. bracteoles]", is a good representation of *Torrubia* for its time, particularly with respect to the fruit with its persistent perianth limb ("*Drupa monosperma . . coronata denticulis corollae, quae evadit pulposa*"), and the persistent style crowned by a penicillate stigma. With the exception of the supernumary bracteoles, the figure of the flower also is good, showing the spreading perianth limb characteristic of so many South American Torrubias, and the widely exserted style and penicillate stigma. The single species described by Aublet, *G. guianensis*, perhaps is conspecific with *Torrubia eggersiana* (Heimerl) Standl.

Perhaps too many transfers from *Pisonia* to *Torrubia* already have been made by Britton and by Standley, and one might be inclined to submit *Torrubia* as a candidate for conservation over *Guapira* in order to avoid additional transfers to the latter. I am inclined not to do so, however, for the following reasons. *Torrubia* has not generally been considered as distinct from *Pisonia*, and consequently

the transfers to the former are not in wide use; transfer to *Guapira* therefore would entail little mental adjustment and inconvenience at this date. Both *Torrubia* and *Guapira* are based upon rather inadequate antique illustrations, but those of the latter are definitely more capable of critical interpretation than the former; it furthermore will be much easier to associate G. *guianensis* with a modern species than *T. opposita* Vell.

a. Anthocarps globose or subglobose; pistillate perianths about 2 mm. long, the limb spreading; stamens about half exserted; leaves predominantly elliptic and acuminate..... 1. G. COSTARICANA

aa. Anthocarps oblong-fusiform; pistillate perianths about 3 mm. long, the limb erect; stamens about one-third exserted; leaves predominantly obovate and obtuse..... 2. G. STANDLEYANA

1. GUAPIRA **costaricana** (Standl.) Woodson, comb. nov.

Torrubia costaricana Standl. in Contr. U. S. Nat. Herb. 13:385. 1911.

Small dioecious trees to 10 m. tall. Branches moderately stout, glabrous, prominently lenticellate at maturity. Leaves rather crowded, petiolate, the blade predominantly elliptic to oblong-elliptic, acuminate, obtuse at the base, 2.5–10.0 cm. long, 1.5–4.5 cm. broad, subcoriaceous, glabrous, the petiole 0.5–1.0 cm. long. Inflorescences 3–6 cm. long, rather shortly pedunculate, many-flowered, minutely puberulent, conspicuously accrescent in fruit, the flowers sessile. Staminate perianth campanulate, about 3 mm. long, about 0.5 mm. in diameter at the base and 2 mm. at the orifice, minutely puberulent, greenish white or yellow, the stamens about half exserted. Pistillate flowers tubular-campanulate, the limb slightly spreading, about 2 mm. long and 0.5 mm. in diameter, minutely puberulent-papillate. Anthocarps globose or subglobose, about 7–8 mm. long, black or purple when ripe.

Costa Rica and Panama, in forests and savannas, sea level to 1000 m.

CHIRIQUÍ: Boquete, *Davidson 689*; David, *Pittier 3370*. COCLÉ: Valle de Antón, *Bro. Maurice 777*; north rim of El Valle, *Alston & Allen 1847*; region north of El Valle de Antón, trail to Las Minas, *Allen 2472*.

Brother Maurice reports the vernacular names of *llanto* and *mala sombra*. *Guapira costaricana* is widely distributed also on the Pacific slope of Costa Rica. In both countries the leaves of plants growing at higher elevations seem broader and more elliptic than those of lower elevations. The fruit, however, is relatively constant.

2. GUAPIRA **standleyana** Woodson, spec. nov.

Arbor dioica usque ca. 10 m. alta. Ramuli graciliusculi indistincte lenticellati juventate tenue puberuli mox glabrati. Folia densiuscula sed mox decidua petiolata lamina praecipue obovata vel obovato-elliptica brevissime acuminata vel obtusa basi latiuscule cuneata 3–15 cm. longa 1–6 cm. lata firmiter membranacea glabra petiolo 0.5–1.0 cm. longo. Inflorescentiae 4–8 cm. longae minute puberulae in fructu paulo accrescentes floribus sessilibus vel subsessilibus. Perianthium masculum campanulatum ca. 3.5 mm. longum faucibus ca. 2 mm. diam. minute

Fig. 125. *Guapira costaricana*

puberulo-papillatum staminibus ca. tertio exsertis. Perianthium femineum tubulosum limbo erecto vel fere erecto ca. 3 mm. longum et 0.5 mm. diam. minute puberulum. Anthocarpia oblongo-ellipsoidea 10–13 mm. longa ca. 6–7 mm. lata rubra (aetate immatura?).

Panama, in savannas and bush, near sea level.

CANAL ZONE: near Gorgas Memorial Laboratory [Cocoli], *P. White 109*; bank of Río Cocoli, *P. White 104*. PANAMÁ: sabanas north of Panama City, *Bro. Paul 467*; Taboga Island, *Pittier 3544* (US, HOLOTYPE; F); vicinity of Juan Franco Race Track, near Panamá, *Standley 27747*; between Las Sabanas and Matías Hernández, *Standley 31823*. SAN BLAS: forests around Puerto Obaldía, *Pittier 4316*. PROVINCE UNKNOWN: *Seemann s. n. pro parte*.

Sharply distinguished from *G. costaricana* because of the rather narrow oblong-ellipsoid fruit. Two dupla of the Seemann collection seen in the herbarium of the New York Botanical Garden and the Gray Herbarium consist of mixtures; the former of *Guapira standleyana* and *Neea delicatula,* and the latter of *Guapira standleyana, Neea delicatula,* and *Pisonia aculeata.* This mixture may be responsible for Seemann's remarks on the "hermaphrodite" flowers of his collection, which he cited under *Pisonia pacurero* HBK., and the difficulty of distinguishing *Neea* from *Pisonia* (Seemann, in Bot. Voy. Herald, p. 192. 1854). Seemann's plate of *P. pacurero* clearly is a pistillate *Neea,* although not definitely *N. delicatula.* Seemann cited his collection from "dark forests, near Cruces."

5. PISONIA L.

Pisonia L. Sp. Pl. 1026. 1753.

Bessera Vell. Fl. Flum. 147. 1825; Icon. 4: *t. 12.* 1841, *nec* Schult, *nec alior.*
Columella Vell. loc. cit. 155. 1825; Icon. 4: *t. 17.* 1841, *nec* Comm. *nec* Lour.
Pallavia Vell. loc. cit. 151. 1825; Icon. 4: *t. 12.* 1841.

Shrubs or small trees, usually scandent and armed with stout axillary spines in our species. Leaves opposite to irregularly approximate. Inflorescences usually terminal on highly modified short shoots, umbelliform or densely corymbiform-thyrsiform. Flowers small, the subtending bracteoles in a more or less contracted spiral upon the pedicel. Staminate flowers campanulate; stamens usually 6–8, unequal, widely exserted, the short tube of the filaments adnate to the stipe of the pistillode. Pistillate flowers tubular, the limb of the perianth apparently always erect, the staminodes reduced to a low, occasionally glandular-dentate disc adnate to the stipe of the pistillode. Anthocarps pentagonal-clavate, coriaceous, armed with longitudinal rows of stipitate glands upon the angles.

Numerous species in the Antilles, Central and South America; southern peninsular Florida; western Africa, southeastern Asia and Oceania. A single species is known from Panama at present.

1. Pisonia aculeata L. Sp. Pl. 1026. 1753.

Pisonia villosa Poir. in Lam. Dict. 5:347. 1804.
Pisonia sieberi Schlecht. in Linnaea 12:876. 1822.
Pisonia loranthoides HBK. Nov. Gen. & Sp. 7:197. 1825.
Pisonia monotaxadenia Wright, ex Sauv. in Anal. Acad. Cien. Habana 7:199. 1870.
Pisonia grandifolia Standl. in Contr. U. S. Nat. Herb. 13:391. 1911.

Divaricately branched shrub or woody liana, usually armed with stout recurved axillary spines, glabrous to densely pubescent. Leaves opposite to irregularly approximate, the blade very variable in shape and size, usually obovate to obovate-elliptic, acute to acuminate, 2–10 cm. long, 1–5 cm. broad, the petiole 1–3 cm. long. Inflorescences usually borne at the tips of greatly condensed short shoots, umbelliform or densely corymbiform-thyrsiform, rather shortly pedunculate, 3–6 cm. long, greatly accrescent and expanded in fruit, many-flowered. Staminate flowers campanulate, greenish yellow, about 3 mm. long, about 2 mm. in diameter at the orifice of the limb, minutely puberulent-papillate without, the stamens

Fig. 126. Pisonia aculeata

widely exserted. Pistillate flowers tubular to somewhat urceolate, about 2.5 mm. long and 1 mm. in diameter, the limb erect, the stigma and style widely exserted. Anthocarps borne upon greatly elongate pedicels, pentagonal-clavate, 7–9 mm. long, 3–4 mm. broad, green, coriaceous, the stipitate glands uniseriate upon the five angles, the sides minutely and densely puberulent.

Very widely distributed in tropical America, and apparently a ruderal introduction in western Africa and southeastern Asia; in rain forests and moist thickets from sea level to about 1000 m.

CANAL ZONE: Barro Colorado Island, *Standley 40933*, *Standley 40918*. COCLÉ: hills north of El Valle de Antón, *Allen 2835*. PANAMÁ: Juan Díaz, *Standley 30472*; Río Tapía, *Standley 28251*. PROVINCE UNKNOWN: *Seeman s. n. pro parte*.

This species must be very much more frequent than the records would indicate. It is popularly known as *uña de gato*, in allusion to the stout recurved thorns.

BATIDACEAE

Batis maritima L. is to be expected in Panama. This dioecious herbaceous to fruticose plant with opposite, simple, entire and sessile leaves is the sole species of the family. It is an inhabitant of the beaches of subtropical and tropical America and the Hawaiian Islands.

PHYTOLACCACEAE

By KATHERINE RAEDER

Herbs, shrubs or trees, often vines. Leaves simple, entire, alternate, petiolate or subpetiolate, with or without stipules. Inflorescence in terminal or extra-axillary racemes, although occasionally axillary. Flowers bisexual or unisexual by reduction, actinomorphic; perianth monochlamydeous; tepals generally 4–5, free or slightly connate at the base, usually persistent in fruit; stamens 3–many, often varying in number within the same species, frequently borne on a hypogynous disc in 1 or 2 cycles opposite or alternate with the tepals, the filaments free or basally connate; ovary superior, rarely inferior, 1- to 16-carpellate, the carpels free to partly or entirely connate, the styles when present as many as the carpels, usually terminal, sometimes subterminal, generally free but occasionally united, the stigma capitate, or sessile and penicillate; ovules basal, campylotropous, solitary. Fruit a berry, drupe, or achene, the seeds 1–many. Embryo coiled or bent around the perisperm.

a. Flowers subsessile in terminal or axillary racemes; tepals persistent in fruit, erect; fruit an achene..... 1. Petiveria
aa. Flowers obviously pedicellate; tepals persistent in fruit (except in *Phytolacca rivinoides*), reflexed, erect, or spreading; fruit a berry or drupe.
  b. Tepals 5; ovary 2- to many-carpellate.
    c. Ovary 6- to 15-carpellate; styles free but connivent; stamens 6–33; fruit a many-seeded berry..... 2. Phytolacca
    cc. Ovary 2-carpellate; styles 2, free and recurved; stamens 3–9, usually 5; fruit a 1-seeded drupe..... 3. Microtea
  bb. Tepals 4; ovary 1-carpellate.
    d. Tepals erect in fruit; stamens 4; fruit a berry..... 4. Rivina
    dd. Tepals spreading or reflexed in fruit; stamens 8 (–25); fruit a drupe..... 5. Trichostigma

1. PETIVERIA L.

Petiveria L. Sp. Pl. 342. 1753.

Tall herbs, sometimes woody at the base. Leaves alternate, simple, entire, petiolate, minutely stipulate. Inflorescence an elongate terminal or axillary raceme, the flowers small, subsessile, bracteate and bracteolate. Tepals 4, united into a short tube, the lobes subequal, linear, persistent and erect in fruit. Stamens 8, inserted irregularly on a hypogynous disc at the base of the ovary, the filaments filiform and of varying lengths, the anther linear, dorsifixed. Ovary 1-carpellate,

Fig. 127. *Petiveria alliacea*

oblong, tomentose, 4- to 6-uncinate, the stigma 1, sessile, penicillate, decurrent along the ventral margin of the ovary, the ovule 1, basifixed. Fruit a linear achene; pericarp coriaceous and adherent to the seed. Seed 1, linear, the testa membranous, the albumen scanty and mealy, the cotyledons foliaceous.

Two species in the Western Hemisphere.

1. Petiveria alliacea L. Sp. Pl. 342. 1753.

Petiveria octandra L. Sp. Pl. 486. 1762.
Petivera foetida Salisb. Prodr. 214. 1796.
Petiveria alliacea β *grandifolia* (L.) Moq. in DC. Prodr. 13²:9. 1849.
Petiveria alliacea γ *octandra* (L.) Moq. loc. cit. 1849.
Petiveria ochroleuca Moq. loc. cit. 1849.
Petiveria paraguayensis Parodi, in Anal. Soc. Cient. Argent. 160. 1878.
Petiveria hexandria Sesse & Moc. Fl. Mex. ed. 2. 90. 1894.

Tall herbs, often woody at the base, with slender sometimes angled stems, to 5–10 dm. tall, with a strong odor of garlic. Leaves elliptic to obovate, the apex acute or acuminate, often mucronate, the base narrowed, 5.5–16.0 cm. long, about 2–6 cm. broad, slightly pubescent; petioles 1.5–2.0 cm. long. Inflorescence in slender usually sparsely flowered racemes 15–40 cm. long; pedicels up to 1 mm. long. Tepals white or greenish-white, sometimes pale pink, often basally pubescent, about 3–5 mm. long. Stamens 8, free, up to 3 mm. long. Ovary 4-uncinate, the hooks becoming elongate and quite prominent in fruit. Fruit linear, 8 mm. long.

United States, Florida to Texas; throughout the West Indies and Central America; South America, Colombia to Argentina; common in dry or moist fields and forests, often found near habitations, especially on waste ground, up to 1500 meters. Some of the common names are: Garlic-weed, Obeah-bush, Anomu, and Guinea-hen weed.

Bocas del Toro: Chiriquí Lagoon, *Von Wedel 1323*; Water Valley, *Von Wedel 636*. Chiriquí: Puerto Armuelles, *Woodson & Schery 841, 900*; between Remedios and David, *P. White 308*; Río Dupí, *Pittier 5222*. Canal Zone: Ancón Hill, *Standley 26336*; Las Cruces Trail, Government forest, *Hunter & Allen 731, 694*. Panamá: Taboga Island, *Allen 1291; Standley 27838, 27025; Woodson, Allen & Seibert 1470; Macbride 2791*. Darién: Pinogana, *Allen 940*.

Petiveria alliacea closely resembles *P. tetrandra*, a species limited in geographical distribution to Brazil. However, the two may be separated fairly readily by the presence in *P. tetrandra* of 6 hook-like processes in the ovary and fruit rather than the 4 found in *P. alliacea*. Furthermore, the flower pedicels in *P. tetrandra* are about 5 mm. long, whereas those of *P. alliacea* are so short that the flowers appear to be sessile.

2. PHYTOLACCA L.

Phytolacca L. Sp. Pl. 441. 1753.

Sarcoca Raf. Tell. 3:55. 1837.
Pircunia Moq. in DC. Prodr. 13²:29. 1849.

Tall perennial herbs or shrubs. Leaves alternate, simple, entire, petiolate, exstipulate, generally glabrous. Inflorescence a terminal, or extra-axillary raceme;

Fig. 128. *Phytolacca rugosa*

the pedicels basally bracteate, often with 1 or more bracteoles above. Tepals 5, equal, usually glabrous, persistent or deciduous in fruit. Stamens 8–22, inserted at the base of the calyx usually on a hypogynous disc, in 1 or 2 cycles, the filaments free, the anthers dorsifixed. Ovary subglobose, 5- to 16-carpellate, the carpels completely or only partly united, the styles equal in number to the carpels, terminal, generally connivent, often recurved, the ovule solitary in each cavity. Fruit a globose 5- to 16-celled fleshy berry. Seed 1 in each cavity, the endosperm mealy.

About 26 species, tropical and subtropical, mostly in the Americas, some in Africa, Asia, and Asia Minor.

a. Carpels connate at the base, the apices free; styles free; tepals reflexed in fruit..... 1. P. RUGOSA

aa. Carpels completely connate, styles free but connivent; tepals either erect or spreading in fruit, or deciduous.

b. Carpels 6–10; stamens 8–20; tepals erect or spreading in fruit; raceme up to 20 cm. long..... 2. P. ICOSANDRA

bb. Carpels 10–16; stamens 9–22; tepals deciduous in fruit; raceme up to 55 cm. long..... 3. P. RIVINOIDES

1. PHYTOLACCA RUGOSA Br. & Bouché, Ind. Sem. Hort. Berol. 13. 1851. Linnaea 25:297. 1852.

Woody herbs up to 2½ m. tall, the glabrous branches erect and angled. Leaves lanceolate-elliptic, the apex acuminate, the base attenuate, 2–5 cm. broad, 4–14 cm. long. Racemes suberect, terminal or extra-axillary, 4–15 cm. long, the flowers fairly crowded; pedicels about 3.5–4.0 mm. long, the bracts about 4 mm. long, the bracteoles about 1 mm. long. Tepals oblong-elliptic, the apex rounded, white or pink, reflexed in fruit, 2–3 (–4) mm. long. Stamens 6–12 in 1 cycle, inserted on a subhypogynous disc, about 1.5–2.0 mm. long. Ovary subglobose, 6- to 8-carpellate, the carpels free at the apex, the styles equal to the number of carpels and free. Fruit a purple berry, 6–8 mm. in diameter.

In Panama, appearing at 1200–2000 meters; generally somewhat higher altitudes throughout the rest of the range, Mexico southwards to Colombia. The common name is *jaboncillo*.

BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, *Allen 4998*. CHIRIQUÍ: trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, *Allen 1511*; *Seibert 302*; foot of Sierra del Boquete, *Maurice 742*; vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 975*; north forested face of Cerro Copete, eastern spur of Volcán de Chiriquí, *Allen 4871*; vicinity of Callejón Seco, Volcán de Chiriquí, *Woodson & Schery 480*; trail from Bambito to Cerro Punta, *Allen 311*.

P. rugosa is distinguished from *P. icosandra* by the incomplete union of the carpels, the shorter racemes, and the tendency towards fewer stamens and carpels. The free apices of the carpels may be observed equally well in flower or in fruit. The styles of the flower are fairly close together, but are definitely free and not connivent; in fruit they are pulled farther apart by the expansion of the seeds within the carpels. The staminal cycle is generally considered to be the inner one, the outer cycle having been suppressed. As in most species of *Phytolacca* the number of stamens is variable, fluctuating even between flowers of the same inflorescence.

2. PHYTOLACCA ICOSANDRA L. Syst. ed. 10. 1040. 1849.

Phytolacca malabarica Crantz, Inst. 2:484. 1769.
Phytolacca mexicana Crantz, loc. cit. 1769.
Phytolacca mexicana Gaertn. Fruct. 1:377. 1788.
Phytolacca triquetra Moench, Meth. Suppl. 107. 1802.
Phytolacca bogotensis HBK. Nov. Gen. et Spec. 2:183. 1823.
Phytolacca sessiliflora Kunth & Bouché, Ind. Sem. Hort. Berol. 15. 1848 Ann. Sci. Nat. III. 11:230. 1849.
Phytolacca acuminata Hort. ex Moq. in DC. Prodr. 13^2:33. 1849.
Phytolacca longespica Moq. loc. cit. 1849.
Phytolacca purpurascens A. Br. & Bouche, Ind. Sem. Hort. Berol. 13. 1851. Linnaea 25: 297. 1852.
Phytolacca macrostachya Willd. ex J. A. Schmidt, in Mart. Fl. Bras. 14^2:344. 1872.
Phytolacca nova-hispania Millsp. in Field Mus. Publ. Bot. 2:41. 1900.
Phytolacca icosandra var. *angustitepala* H. Walt. in Englr. Pflanzr. 4^{83}:61. 1909.
Phytolacca icosandra var. *sessiliflora* H. Walt. loc. cit. 1909.

Stout herbs 1–2 meters tall, sometimes rather succulent, with sharply angled and often pubescent branches. Leaves narrowly elliptic or sometimes ovate-elliptic, the apex acute, the base narrowed and decurrent along the petiole, 6.5–15 cm. long, 2.3–5.0 cm. broad. Inflorescence an elongate pubescent raceme of densely crowded flowers, 16–30 cm. long; pedicels 1–1.5 mm. long; bracts lanceolate-linear, 3–4 mm. long, the bracteoles about 0.8 mm. long. Tepals broadly elliptic or obovate, the apex rotund, pink, white, or sometimes greenish, occasionally pubescent, 2.5–3.5 mm. long. Stamens 8–20, inserted in 2 cycles on a disc at the base of the perianth, about 3 mm. long. Ovary 6–8 carpellate, the carpels completely united, the styles free but connivent, often recurved. Fruit a subglobose purple berry 6–8 mm. in diameter. Seed shiny black.

Mexico, the West Indies, Central America south to Ecuador. Most commonly found up to 1450 meters in Panama. The common name is *jaboncillo*.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 401*.

The taxonomic controversy over this perplexing species has probably arisen from the variability of the distinguishing characters. The single most distinctive consideration which separates it from *P. rugosa* is that of whether or not the carpels of the ovary are entirely connate. To the unpracticed eye this is a tricky character, but it is the most reliable. The connivent styles are the best clue to the united carpels, as even in fruit they are closely clustered at the center of the berry in spite of the expansion of the ovary which would tend to pull them outwards. The remaining separative characters are best expressed as strong tendencies. The pedicels vary in length but in the Panamanian representatives are usually about 1 mm. long. The number of carpels may vary from flower to flower in the same inflorescence, but 8- to 9-carpellate ovaries are the most common. The racemes tend to be longer than those of *P. rugosa*, and the flowers are often more crowded.

Walter recognizes two varieties of which one, *P. icosandra* var. *sessiliflora* occurs in a limited range. The subsessile flowers he considers to be important enough to afford varietal status. By "subsessile" it is intended that the pedicel is about 1 mm. in length, as no specimens with a shorter pedicel were found. Nearly all individuals

examined had pedicels of 1 mm. which would place them in this category, although the typical variety with a pedicel of about 3 mm. is reportedly widespread throughout Panama. Herbarium sheets from adjoining countries show a gradual tendency toward longer pedicels, and it is probable that this character is expressed by gradual variation, as are so many others.

3. PHYTOLACCA RIVINOIDES Kunth & Bouché, Ind. Sem. Hort. Berol. 15. 1848. Ann. Sci. Nat. III. 11:231. 1849.

Phytolacca icosandra Wright, Mem. 268. 1828, non Linn. (1759).
Phytolacca bogotensis Miq. Ser. exot. *t. 6.* 3. 1842, non HBK. (1823).
Phytolacca icosandra β Fraseri Moq. in DC. Prodr. 13^2:33. 1849.
Phytolacca macrostachya Willd. ex Moq. loc. cit. 1849.
Phytolacca polystigma Benth. ex Moq. loc. cit. 1849.
Phytolacca acuminata Hort. ex Moq. loc. cit. 1849.
Phytolacca polystyla Schomb. ex Moq. loc. cit. 1849.

Woody herbs or weak shrubs up to 5 m. tall, with angled branches. Leaves ovate, elliptic, or even lanceolate, the apex mucronate, sometimes only acuminate, the base tending to be decurrent, 4.5–7.0 cm. broad, 9–17 cm. long, the petioles 0.9–4.5 cm. long. Racemes terminal or extra-axillary, the flowers uncrowded along the axis, 30–55 (–70) cm. long; pedicels 7–12 mm. long, the basal bract subulate, about 1.5 mm. long with 2 bracteoles above. Tepals white to red, sometimes cream, elliptic, about 2 mm. long, deciduous in fruit. Stamens 9–14 (–22), inserted on a hypogynous disc, about 2 mm. long. Ovary globose, 12- to 16-carpellate, the carpels united throughout their length, the styles as many as carpels, connivent, and recurved. Fruit a purple berry 5–6 mm. in diameter.

Throughout the West Indies; Mexico southwards to Bolivia. Found as high as 1680 meters, but generally below 1500 meters. The common name is *jaboncillo*.

BOCAS DEL TORO: Water Valley, *Von Wedel 833, 796*; Chiriquí Lagoon, *Von Wedel 2079, 2631, 1246, 2460, 2704*; Fish Creek Hills, *Von Wedel 2460*; Garay Creek, *2631*. CHIRIQUÍ: Bajo Chorro, Boquete district, *Davidson 153*. PANAMÁ: forests near Arraiján, *Woodson, Allen & Seibert 1392*. COLÓN: around Dos Bocas, Río Fató Valley, *Pittier 4205*. COCLÉ: El Valle de Antón, along Río Indio trail, *Hunter & Allen 313*.

Although *P. rivinoides* appears quite distinct from *P. icosandra* by virtue of its longer pedicels, deciduous tepals, more numerous carpels, smaller fruit and strikingly elongate racemes, nevertheless some specimens were examined which are suspiciously a mixture of greater or lesser degree of the two species. The most easily recognized clue to a questionable individual is a tendency for the pedicels to be longer than normal for *P. icosandra* and shorter than *P. rivinoides*. In combination with this character are usually found intermediate tendencies for raceme length, fruit size, and carpel number. It is interesting to note that even in plants showing extreme tendencies towards *P. rivinoides* the tepals are always persistent. Furthermore, the leaves of many of these intermediates are sometimes larger than found in either of the two species, although this is not always true.

3. MICROTEA Swartz

Microtea Swartz, Prodr. 53. 1788.

Schollera Rohr, in Skirvt, Naturhist. Selsk. Kjoeb. 2:210. 1792.
Ancistrocarpus HBK. Nov. Gen. et Sp. 2:186. *t. 122.* 1817.
Potamophila Schrank, Pl. Rar. Hort. Nom. 2. *t. 63.* 1819.
Ceratococca Willd. in Roem. et Schult. Syst. 6:800. 1820.
Aphanathe Link, Enum. Hort. Berol. 1:383. 1821.

Sprawling, decumbent or sometimes spreading annual herbs. Leaves alternate, simple, entire, petiolate or subpetiolate, exstipulate. Inflorescence extra-axillary or terminal, racemose, shortly pedicellate, bracteate. Flowers minute. Tepals 5, oblong, persistent and erect in fruit. Stamens 5, inserted at the base of the perianth, alternate with the tepals, the filament filiform, the anther dorsifixed.

Fig. 129. *Microtea debilis*

Ovary globose, 2-carpellate, unilocular, the styles 2, basally connate, the ovule 1, basifixed. Fruit a minute drupe, tuberculate, the pericarp adherent to the seed. Seed 1, the testa crustaceous, the embryo bent, the albumen scanty.

About 9 species in the American tropics.

1. Microtea debilis Sw. Prodr. 53. 1788.

Schollera debilis Rohr, in Skirvt, Naturh. Selsk. Kjoeb. 2:210. 1792.
Microtea ovata Delile, Hort. Monsp. 1827. ex Moq. in DC. Prodr. 13^2:17. 1849.
Microtea debilis α ovata Moq. loc. cit. 1849.
Microtea debilis β rhombifolia Moq. loc. cit. 1849.

Decumbent herbs to 50 cm., the stems sharply angled. Leaves elliptic to ovate, the apex acute, sometimes mucronate, the base attenuate, 1.0–2.3 cm. wide, 1.3–3.6 cm. long, glabrous. Inflorescence a many-flowered raceme 1.5–3.5 cm. long; bracts membranaceous, persistent, about 1 mm. long; pedicels about 1.0 mm. long. Tepals 5, lanceolate, white, about 0.5–0.7 mm. long. Stamens about 0.4 mm. long. Ovary globose, about 0.5 mm. in diameter. Fruit with the tubercles united into a honeycomb like pattern, 1.0–1.5 mm. in diameter.

Throughout the West Indies; from Guatemala southward to Peru and Brazil.

Canal Zone: Chagres, *Fendler 109*; hills between Río Grande and Pedro Miguel on road to Arraiján, *Pittier 2709*; Frijoles, *Standley 31470*; vicinity of Summit, *Standley 30145, 26968*; Balboa, *Standley 25826*; Gatún, *Bro. Heriberto 115*. Bocas del Toro: Changuinola Valley, *Dunlap 402*. Panamá: Chepo, *Pittier 4457*; Panama City, *Bro. Paul 166*; Taboga Island, *Standley 27088*; Exposición, *Bro. Heriberto 277*. Darién: Boca de Cupe, *Allen 883*.

Microtea is a striking genus not only because of the extremely minute flowers, but also because the flowers seem to demonstrate a very much simplified flower plan. The relationship of *Microtea* to the rest of the family is obvious but it also suggests close affinity to some members of the Chenopodiaceae, particularly to the genus *Chenopodium*. Although the number of stamens are usually equal to and alternate with the petals, occasionally 8 stamens will be found irregularly inserted. The tubercles vary in length, and although usually rather short, may be as long as 0.5 mm.

4. RIVINA L.

Rivina L. Sp. Pl. 121. 1753.

Tithona L. Syst. ed. 1. 1735.
Rivinia L. Gen. Pl. ed. 5. 57. 1754.
Piercea Mill. Gard. Dict. ed. 7. 1759.
Solanoides Moench, Meth. 307. 1794.
Tithonia L. ex O. Kuntze, Rev. Gen. 2:552. 1891, sphalm.

Tall often woody herbs, frequently shrub-like, erect or straggling. Leaves alternate, simple, entire, petiolate, exstipulate. Inflorescence a suberect many-flowered terminal or axillary raceme. Flowers small, pedicellate. Tepals 4, subequal, obovate-oblong, rounded or pointed at the apex, persistent and erect or spreading in fruit. Stamens 4, inserted at the base of the perianth in 1 cycle alternate with the tepals, the filaments free, the anther dorsifixed. Ovary

Fig. 130. *Rivina humilis*

1-carpellate, the style subterminal, short, curved, the stigma capitate, the ovule 1. Fruit a globose red berry, the pericarp adherent to the seed, the testa crustaceous.

Three species in the American tropics and subtropics, introduced into Asia and Australia.

1. Rivina humilis L. Sp. Pl. 122. 1753.

Rivina humilis α *canescens* L. Sp. Pl. 122. 1753.
Rivina humilis δ *glabra* L. loc. cit. 1753.
Rivina laevis L. Mant. 41. 1767.
Piercea glabra Mill. Gard. Dict. ed. 8. *Piercea* no. 1. 1768.
Piercea tomentosa Mill. Gard. Dict. ed. 8. *Piercea* no. 2. 1768.
Rivina viridis Schmidt, in Mayer, Samml. Phys. Aufs. 1:185. 1791.
Rivina brasiliensis Nocca, in Usteri. Ann. Bot. 6:63. 1793.
Solanoides pubescens Moench, Meth. 307. 1794.
Solanoides laevis Moench, loc. cit. 1794.
Rivina pallida Salisb. Prod. 67. 1796.
Rivina gracilis Salisb. loc. cit. 1796.
Solanoides undulata Moench, Meth. Suppl. 106. 1802.
Rivina lanceolata Willd. Enum. Hort. Berol. Suppl. 8. 1813.
Rivina tetrandra Desfl. Tabl. ed. 2. 49. 1815.
Rivina puberula HBK. Nov. Gen. & Sp. 2:184. 1817.
Rivina tinctoria Ham. ex G. Don. in Loud. Hort. Brit. Suppl. 1:598. 1832.
Rivina portulaccoides Nutt. in Trans. Am. Phil. Soc. II. 5:167. 1837.
Rivina acuminata Raf. New Fl. 4:13. 1838, non HBK. (1817).
Piercea acuminata Raf. loc. cit. 1838.
Rivina obliquata Raf. loc. cit. 1838.
Piercea obliquata Raf. loc. cit. 1838.
Rivina canescens G. Don. in Steud. Nom. Bot. ed. 2. 2:460. 1841.
Rivina laevis β *acuminata* Moq. in DC. Prodr. 13^2:12. 1849.
Rivina orientalis Moq. loc. cit. 1849.
Rivina procumbens Ruiz, ex Moq. loc. cit. 13. 1849.
Rivina humilis α *puberula* (HBK.) Moq. loc. cit. 1849.
Rivina humilis β *canescens* (G. Don.) Moq. loc. cit. 1849.
Rivina humilis γ *plumbaginifolia* Willd. ex Moq. loc. cit. 1849.
Rivina aurantiaca Warsz. ex Schenk, Ind. Sem. Werceburg. 1861.
Rivina laevis var. *pubescens* Griseb. Fl. Brit. W. Ind. 59. 1864.
Rivina viridiflora Bel, Anal. Soc. Esp. Hist. Nat. 12:105. 1883.
Rivina paraguayensis Parodi, in Anal. Soc. Cient. Argent. 5:206. 1878.
Tithonia humilis O. Kuntze, Rev. Gen. 552. 1891.
Tithonia humilis var. *canescens* f. *albiflora* O. Kuntze, loc. cit. 1891.
Tithonia humilis var. *glabra* O. Kuntze, loc. cit. 1891.
Rivina humilis laevis Millsp. in Field Mus. Publ. Bot. 2:41. 1900.
Rivina humilis var. *orientalis* (Moq.) H. Walt. in Engl. Pflanzenr. 4^{83}:105. 1909.

Straggling shrubs or tall herbs sometimes woody at the base, up to 10 meters high. Leaves elliptic to ovate or lanceolate, the apex acute to acuminate, the base rounded or truncate, 2–6 cm. wide, 4–12 cm. long; petioles 0.6–11.0 cm. long. Flowers small, drooping; pedicels 3 mm. in flower, elongating to about 7 mm. in fruit; bracts lanceolate, about 2 mm. long; tepals 4, white or pinkish white, 2.0–3.5 mm. long; stamens 4, inserted at the base of the perianth, about 1.5 mm. long. Fruit a scarlet or red berry, about 4.0–4.5 mm. in diameter.

Florida to Oklahoma and Texas; throughout Mexico and southward to Argentina; West Indies. In Costa Rica found up to 1040 meters elevation. Particularly common on waste ground, often on coastal rocks. Among the common names are Wild Tomato, Bloodberry, and *carmin*.

BOCAS DEL TORO: region of Almirante, *Cooper 77*; location not stated, *Carleton 52*; vicinity of Nievecita, *Woodson & Schery 1023; Woodson, Allen & Seibert 1807*; Water

Valley, *Von Wedel 609*; Chiriquí Lagoon, vicinity of Little Bocas, *Von Wedel 2526*; vicinity of Chiriquí Lagoon, Big Bight, *Von Wedel 2882*. CHIRIQUÍ: valley of upper Río Chiriquí Viejo, *P. & G. White 88*. COCLÉ: mountains beyond La Pintada, *Hunter & Allen 570*. DARIÉN: near mouth of Río Yapé, *Allen 336*; vicinity of Boca de Cupe, *Allen 889*.

Walter recognizes three varieties of *Rivina humilis* based on glabrity or degree of pubescence. *R. humilis* var. *orientalis* is in Asia, presumably escaped from cultivation as the genus is probably not indigenous to the region. *R. humilis* var. *canescens* is recognized by the tomentose stems and densely pilose leaves and petioles, and is cited as found in Brazil and the lesser Antilles. *R. humilis* var. *glabra* is, as the names implies, completely glabrous, and is widely distributed from Texas to Argentina. Use of pubescence as a distinguishing varietal character is unconvincing; consequently the specimens examined have been treated as a single species with a wide range of variation in the degree of relationship between pubescence and glabrity of any part of a plant. The synonymy has likewise been regarded as pertaining to a single species.

5. TRICHOSTIGMA A. Rich.

TRICHOSTIGMA A. Rich. in Sagra, Hist. Cuba 10:306. 1845.

Villamilla R. & B. ex Benth. & Hook. Gen. Pl. 3:81. 1880.

Woody vines, shrubs. Leaves alternate, simple, entire, petiolate; stipules minute and deciduous. Inflorescence a many-flowered terminal or extra-axillary raceme, the bracts deciduous. Tepals 4, subequal, persistent and reflexed in fruit. Stamens 8–10 (–12), inserted on a hypogynous disc, the filaments free, the anther dorsifixed. Ovary 1-carpellate, unilocular, subglobose, the stigma sessile or subsessile, often penicillate, the ovule 1. Fruit a globose drupe, the pericarp adherent to the seed. Seed 1, the testa crustaceous.

Three species in tropical America.

a. Flowers in crowded condensed racemes; stamens 8–12; pedicels 7–9 mm. long..... 1. T. OCTANDRUM
aa. Flowers in elongate lax racemes; stamens 20–25; pedicels 8–16 mm. long..... 2. T. POLYANDRUM

1. TRICHOSTIGMA OCTANDRUM (L.) H. Walt. in Engl. Pflanzenr. 4^{83}:109. 1909.

Rivina humilis β scandens L. Sp. Pl. 122. 1753.
Rivina octandra L. Cent. Pl. 2:9. 1756.
?*Rivina dodecandra* Jacq. Obs. Bot. 1:6. 1764.
Rivina scandens Mill. Gard. Dict. ed. 8. *Rivinia* no. 2. 1768.
Rivina Mutisii Willd. ex Schult. Mant. 3:305. 1827.
Rivina americana Raf. Fl. Tell. 3:56. 1837.
Trichostigma rivinoides A. Rich. in Sagra. Hist. Cuba. 10:306. 1845.
Rivina octandra β obtusifolia Moq. in DC. Prodr. 13^2:11. 1849.
Rivina Ehrenbergiana Klotzsch, ex Moq. loc. cit. 1849.
Rivina Moritziana Klotzsch, ex Moq. loc. cit. 1849.
Villamilla octandra Hook. f. in Benth. & Hook. Gen. Pl. 3:81. 1880.

Decumbent or suberect shrubs or woody vines up to 10 meters. Leaves oblong to elliptic, the apex acute to acuminate, the base rounded or acute, 3.8–5.5 cm. broad, 12.4–14.7 cm. long; petioles 2.4–3.7 cm. long, glabrous. Inflorescence a

Fig. 131. *Trichostigma polyandrum*

fairly dense many-flowered raceme, about 5.0–6.5 (–11.0) cm. long; pedicels 3–9 mm. long; bracts lanceolate, 2 mm. long, deciduous, the bractlets triangular, 0.5 mm. long. Tepals white to whitish-green, 2–3 mm. long. Stamens 8–12, inserted irregularly at the base of the perianth, 3–4 mm. long. Fruit a subglobose drupe, black, 5.5–6.0 mm. in diameter.

United States (southern peninsular Florida and the Keys); West Indies; throughout Mexico and Central America; South America (Venezuela to Argentina); common in abandoned fields and moist woods.

CANAL ZONE: drowned forest of upper Río Pequeni between Salamanca Hydrographic Station and Río Boquerón, *Allen 17279*. DARIÉN: Tucuti, *M. E. & R. A. Terry 1396*.

The Terrys have stated on the specimen label that *T. octandrum* is a tree, but there are no other indications that trees are even found in this genus. *T. octandrum* occurs as a woody shrub or liana sprawling over adjacent shrubs and trees.

2. TRICHOSTIGMA POLYANDRUM (Loesener) H. Walt. in Engl. Pflanzenr. 4^{83}:112. 1909.

Rivina polyandra Loesener, in Engl. Bot. Jahrb. 23:123. 1896.
Villamilla polyandra H. Walt. loc. cit. 37: Beibl. 83:24. 1906.

Weak shrubs up to 5 meters, or woody vines climbing on shrubs. Leaf blades elliptic to ovate, the apex acute to attenuate, the base rounded or acute, 7.0–16.8 cm. long, 3.5–6.6 cm. broad, the petioles 1.0–3.0 cm. long, glabrous. Inflorescence a long uncrowded raceme, about 8.0–21.0 cm. long; pedicels 8–16 mm. long; bracts lanceolate, 1.5–2.0 mm. long, deciduous, the bractlets about 0.5 mm. long. Tepals white in flower, red, purple or purplish-pink in fruit, 4.0–9.0 mm. long. Stamens 20–25 inserted at the base of the perianth. Ovary subglobose, the style very short. Fruit a drupe, purple or red, 4.5–5.5 mm. in diameter.

Central America (Nicaragua, Costa Rica and Panama).

BOCAS DEL TORO: Pumpkin River near Chiriquí Lagoon, *Von Wedel 2571*; Water Valley, *Von Wedel 926, 1439, 714, 1547, 940*; *Woodson, Allen & Seibert 1832*; Almirante, *Cooper 133*. PANAMÁ: Río Juan Díaz above Juan Díaz, *Allen 944*.

Trichostigma appears to have close affinities with *Rivina*. However the two may easily be distinguished by the more numerous stamens, the tepals reflexed in fruit, the terminal stigma, the deciduous stipules, and the drupaceous fruit of *Trichostigma*. The genera have been treated as one genus by some authors, but recently they have been regarded as separate.

AIZOACEAE

By LORIN I. NEVLING, Jr.

Annual or perennial herbaceous or suffruticose plants, prostrate or upright, often succulent. Leaves usually simple, alternate, opposite or pseudoverticellate, often fleshy, sometimes reduced to scales, entire; stipules scarious or absent. Inflorescences axillary or terminal, modified cymes or the flowers solitary. Flowers bisexual, polygamodioecious or unisexual, actinomorphic, often small. Perianth monochlamydeous, usually 4- or 5-parted, free or connate, sometimes appendaged on the outer surface, often persistent in fruit. Stamens (3), 4, 5 or many, the outermost often sterile and petaloid (but not in our species), the filaments free or variously connate at the base into fascicles or into a monadelphous sheath, free or adnate to the perianth, the anthers oblong or linear, small, dehiscing longitudinally. Pistil 1, the ovary superior to inferior, 1–5 (–20) loculate, the placentation axile, parietal or basal, the ovules solitary to many per locule, anatropous or campylotropous, the styles as many as the locules. Fruit a loculicidal or circumscissile capsule or indehiscent and either baccate or nut-like; seed with mealy endosperm, sometimes strophiolate, the embryo curved.

A large weedy family particularly well-developed in South Africa. Three genera are represented in Panama, each by a single species. A fourth genus, *Glinus*, with a single species [*G. radiatus* (Ruiz & Pav.) Rohrb.] has been reported from Panama. I have been unable to locate a voucher for this record but have included the genus in the key to genera.

This study is based primarily on the work of F. Pax and K. Hoffman (in Natur-Pflanzenf. 16^c:179–233. 1934) and P. Wilson (in North Amer. Fl. 21:267–277. 1932).

a. Leaves basal or pseudoverticellate, not fleshy; tepals distinct to the base or nearly so, with or without appendages on the outer surface beneath the apex; fruit a loculicidal capsule, 3- to 5-loculate; seeds strophiolate or estrophiolate.
  b. Plants glabrous; leaves generally linear; flowers pedicellate; tepals distinct to the base, without appendages; seeds estrophiolate..... 1. Mollugo
  bb. Plants tomentulose; leaves obovate, oblanceolate or rounded-spatulate; flowers sessile or short-pedicellate; tepals distinct to the base or nearly so, with appendages; seeds strophiolate..... Glinus
aa. Leaves opposite, fleshy; tepals connate, with appendages on the outer surface beneath the apex; fruit a circumscissile capsule, 1- to 5-loculate; seeds estrophiolate.
  c. Leaves obovate to rounded-spatulate, strikingly unequal; ovary 1- or 2-loculate; styles 1 or 2; seeds few..... 2. Trianthema
  cc. Leaves linear, elliptic or narrowly obovate, more or less equal; ovary 3- to 5-loculate; styles 3 to 5; seeds numerous..... 3. Sesuvium

1. MOLLUGO L.

Mollugo L. [Gen. 356. 1737]; Sp. Pl. 89. 1753.

Galiastrum Heist. ex Fabricius, Enum. Pl. Hort. Helmst. 108. 1759.
Lampetia Raf. Fl. Tellur. 3:34. 1836.

Fig. 132. ***Mollugo verticellata***

Herbaceous or suffruticose plants, glabrous throughout. Leaves simple, basal or pseudoverticellate, generally linear; stipules deciduous. Inflorescences axillary, cymose. Flowers bisexual, pedicellate. Perianth 5-parted, distinct to the base, imbricate, scarious at the margins, lacking appendages. Stamens 3–10, united at the base. Ovary superior, 3- to 5-loculate, the ovules campylotropous, numerous on the axile placenta. Capsule loculicidal; seeds generally numerous, small, estrophiolate.

About 25 species in the temperate and tropical regions of both hemispheres.

1. MOLLUGO VERTICELLATA L. Sp. Pl. 89. 1753.

Pharnaceum hoffmannseggianum Roem. & Schult. Syst. Veg. 6:692. 1820.
Mollugo dichotoma Schrank, Pl. Rar. Hort. Monac. *t. 64.* 1821.
Mollugo arenaria HBK. Nov. Gen. & Sp. 6:20. 1823.
Mollugo hoffmannseggiana (Roem. & Schult.) Ser. in DC. Prod. 1:393. 1824.
Mollugo schrankii Ser. loc. cit. 391. 1824.
Pharnaceum verticellatum (L.) Spreng. Syst. 1:949. 1825.
Pharnaceum arenarium (HBK.) Spreng. loc. cit. 1825.
Mollugo juncea Fenzl, in Ann. Wien Mus. 1:378. 1836.
Mollugo diffusa Willd. ex Fenzl. loc. cit. 377. 1836, nom. nud. in syn.
Mollugo spergulaefolia Willd. ex Fenzl, loc. cit. 378. 1836, nom. nud. in syn.
Mollugo triphylla Schrank, ex Steud. Nom. ed. 2. 2:154. 1841, nom. nud. in syn.
Mollugo gracillima Anders. in Vet. Akad. Handl. Stockh. 1853:226. 1855.
Pharnaceum cerviana Mart. ex Rohrb. in Mart. Fl. Bras. 14^2:241. 1872, non L., nom. nud. in syn.
Mollugo axillaris Schlecht. ex Rohrb. loc. cit. 242. 1872, nom. nud. in syn.

Annuals, prostrate to ascending, often falsely dichotomously branched. Leaves pseudoverticellate, 3–6 per node, unequal, generally oblong-linear, 1–3 cm. long, 1–2 mm. broad, more or less acute at the apex, gradually tapered to the base; sessile. Inflorescence axillary, modified cymose; pedicel 3–5 mm. long. Flowers with the tepals elliptic, about 2.0–2.5 mm. long, 0.5–0.75 mm. broad, persistent and subtending the fruit, glabrous; stamens 3, the filaments filiform, to 2 mm. long, connate at the very base, the anthers ovoid, about 0.25 mm. long and broad; ovary ovoid, 3-loculate, 1.0–1.5 mm. long, the styles 3, 0.5–0.75 mm. long, spreading. Capsule ovoid, 2–3 mm. long, about 1.5 mm. in diameter; seeds numerous, reniform, about 0.5 mm. long and broad, the testa with several distinct ridges along the back and sides, brown.

Cosmopolitan weeds in the temperate and tropical regions of the world. This species has a rather large and complex synonomy involving numerous infraspecific categories which are not included here in the synonymy.

CANAL ZONE: Chagres, *Fendler 11*. PANAMÁ: San José Island, *Johnston 1232*.

2. TRIANTHEMA L.

TRIANTHEMA L. Sp. Pl. 223. 1753.

Reme Adans. Fam. 2:245. 1763.
Zaleya Burm. f. Fl. Ind. 110, *t. 31*. 1768.
Papularia Forsk. Fl. Aegypt.-Arab. 69. 1775.
Rocama Forsk. loc. cit. 71. 1775.
Portulacastrum Juss. ex Medic. Phil. Bot. 1:99. 1789.
Zallia Roxb. Fl. Ind. 3:74. 1832.
Ancistrostigma Fenzl, in Ann. Wien Mus. 2:293. 1839.
Racoma Willd. ex Steud. Nom. ed. 2. 2:429. 1841.
Zaleia Steud. loc. cit. 795. 1841.
Pomatotheca F. Müll. Fragm. 10:72. 1876.

Herbaceous or suffruticose plants, branched, upright or prostrate. Leaves simple, opposite, strikingly unequal, fleshy, obovate to rounded-spatulate, the petioles connate into a petiolar sheath surrounding the stem; stipulate. Inflorescences axillary, cymose or the flowers solitary. Flowers bisexual, sessile or pedicellate. Perianth 5-parted, connate below, the lobes appendaged on the outer surface beneath the apex, imbricate. Stamens 5 or more, inserted on the perianth tube or free and monadelphic. Ovary superior, 1- or 2-loculate, the ovules campylotropous, few on the axile placenta, the styles 1 or 2. Capsule circumscissile; seeds few, reniform, the testa often wrinkled, estrophiolate.

About 15 species of the tropics and subtropics.

1. TRIANTHEMA PORTULACASTRUM L. Sp. Pl. 223. 1753.

Trianthema monogynum L. Mant. 69. 1767.
Trianthema procumbens Mill. Gard. Dict. ed. 8. no. 1. 1768.
Portulacastrum monogynum (L.) Medic. Phil. Bot. 1:99. 1789.
Trianthema flexuosa Schum. & Thonn. Beskr. Guian. Pl. 241. 1828.

Fig. 133. *Trianthema portulacastrum*

Herbaceous annuals, erect or prostrate, the young stems sometimes with a decurrent line of hairs from the interpetiolar stipules to the node below and glabrescent, often alternately branched by the development of the axillary bud subtended by the smaller leaf of the nodal pair. Leaves of any pair strikingly unequal, the larger at least twice as large as the smaller, obovate to rounded-spatulate, 1–3 cm. long, 0.5–2.0 cm. broad, acute, obtuse, retuse and often mucronulate at the apex, cuneate at the base, glabrous above and below; petiole 0.3–1.5 cm. long, at the base connate into a sheath surrounding the stem, the interpetiolar stipule deltoid, 1–2 mm. long, remotely serrate or entire. Inflorescence with the flowers solitary; sessile. Flowers with the perianth tube campanulate, often intimately associated with the petiolar sheath of the subtending leaves, the lobes lanceolate, about 1.5 mm. long, 1 mm. broad, glabrous, appendage horn-like, barbed about 0.75 mm. long; stamens 10, inserted at the orifice of the perianth tube, the filaments filiform, about 1.5 mm. long, glabrous, the anthers ovoid, about 0.5 mm. long and broad; ovary turbinate, about 1 mm. long, 1 mm. in diameter, truncate and irregularly fleshy-lobed at the apex, glabrous, the style 1, about 1 mm. long. Capsule almost enclosed in the petiolar sheath, turbinate, about

4.5 mm. long, 3.5 mm. in diameter, sessile, truncate and crested at the apex, circumscissile at about the middle; seeds 2–5, reniform, 1.5–1.75 mm. in diameter, the testa wrinkled, reddish-brown to black.

A pantropic species.

CANAL ZONE: Fort Clayton, *Standley 29003*.

3. SESUVIUM L.

Sesuvium L. Syst. ed. 10. 1058. 1759.

Squibbia Raf. New Fl. 4:16. 1838.
Diplochonium Fenzl, Nov. Stirp. Dec. 57. 1839.
Pyxipoma Fenzl, in Ann. Wien Mus. 2:293. 1839.
Psammanthe Hance, in Walp. Ann. 2:659. 1852.
Halimus O. Ktze. Rev. Gen. 1:263. 1891.

Herbaceous or suffruticose plants, upright or prostrate, sparsely branched. Leaves simple, opposite, more or less equal, fleshy, generally linear, elliptic or narrowly obovate, the petioles clasping or connate and surrounding the stem; estipulate. Inflorescence axillary or rarely terminal, glomerules or the flowers solitary. Flowers bisexual, sessile or pedicellate. Perianth 5-parted, connate below, the lobes generally appendaged on the outer surface beneath the apex, imbricate. Stamens 5, free and alternitepalous, or numerous, and inserted on the perianth tube. Ovary superior, 3- to 5-loculate, the ovules campylotropous, many on the axile placenta, the styles 3 to 5. Capsule circumscissile; seeds numerous, reniform, the testa smooth, estrophiolate.

Six to eight species, tropical and subtropical strand plants of both hemispheres.

1. Sesuvium portulacastrum (L.) L. Syst. Nat. ed. 10. 1058. 1759.

Portulaca portulacastrum L. Sp. Pl. 446. 1753.
Sesuvium revolutifolium Ortega, Dec. 19. 1797.
Sesuvium ortegae Spreng. Bot. Gart. Halle Nachtr. 1:36. 1801.
Sesuvium pedunculatum Pers. Syn. Pl. 2:39. 1806.
Sesuvium sessile Pers. loc. cit. 1806.
Sesuvium sessiliflorum Domb. ex Rohrb. in Mart. Fl. Bras. 14^2:310. 1872, nom. nud. in syn.
Halimus portulacastrum (L.) O. Ktze. Rev. Gen. 1:263. 1891.

Herbaceous perennials, glabrous throughout, the branches trailing and often rooting at the nodes, sometimes rather stout. Leaves linear, elliptic or narrowly obovate, 1–5 cm. long, 0.2–1.0 cm. broad, subacute to acute at the apex, gradually tapered to the base; petiole 1–5 mm. long, dilated at the base and clasping the stem but the sheaths not connate. Inflorescence axillary, the flowers solitary, pink; pedicel 2–11 mm. long. Flowers with the perianth tube obconic to subcampanulate, 1.5–3.0 mm. long, the lobes ovate, 4–7 mm. long, 3.0–4.5 mm. broad, somewhat auriculate at the perianth tube orifice, persistent and somewhat reflexed in fruit, appendage horn-like, 1.0–1.5 mm. long; stamens numerous, inserted at the orifice of the perianth tube, free or subconnate, the filaments 1.5–3.5 mm. long, gradually tapering to the apex, the anthers oblong, 0.5–0.75 mm. long, 0.25–0.5 mm. broad; ovary ovoid to subglobose, 3.0–3.5 mm. long, 2.5–3.0 mm. in diameter,

Fig. 134. *Sesuvium portulacastrum*

the styles 3 or 4, 1.5–3.5 mm. long spreading or erect. Capsule ovoid or obovoid, about 6.5 mm. long, 3 mm. in diameter, circumscissile below the middle; seeds 8–30, lenticular-reniform, about 1.0–1.5 mm. in diameter, the testa smooth, black.

Circumtropical.

BOCAS DEL TORO: bar mouth, Changuinola Valley, *Dunlap 139, Stork 139.* CANAL ZONE: Cristóbal, *Artamanoff s. n.*; Balboa, *Standley 25625, 30882*; railroad and dock yards at Balboa, *Macbride & Featherstone 24*; vicinity of Fort Sherman, *Standley 31180.* COLÓN: vicinity of Palenque, *Pittier 4118.* PANAMÁ: Pearl Islands, *Johansen 111*; Saboga Island, *Allen 2634, Miller 1965*; near Punta Paitilla Military Reservation outskirts of Panama City, *Bro. Maurice 754*; San José Island, *Erlanson 173.* SAN BLAS: forests around Puerto Obaldía, *Pittier 4400.*

PORTULACACEAE

By LORIN I. NEVLING, Jr.

Herbs, subshrubs or shrubs, more or less succulent, often glabrous. Leaves alternate, opposite or in basal rosettes, simple, terete, subterete or plane, often fleshy, pinnately veined; stipules scarious, fimbriate, tufted or rarely absent. Inflorescence terminal or axillary, paniculiform, racemose, cymose or the flowers solitary. Flowers bisexual, often insignificant. Sepals (involucral bracts) 2 or

rarely 4–8, connate at the base or free, persistent or caducous, scarious or herbaceous, imbricate. Petals (tepals) 4–5 or rarely fewer or more, connate at the base or free, deciduous or rarely calyptrate, imbricate. Stamens often as many as the petals and opposite them, sometimes fewer or more, free or basally adnate to the corolla, the filaments filiform, the anthers 2-celled, dehiscing longitudinally, introrse. Pistil 1; ovary superior to inferior, becoming uniloculate, the placentation central, basal, the ovules (1–) 2–many, campylotropous; styles and stigmas 1–9, united below or free. Fruit capsular, circumscissily or loculicidally dehiscent, rarely indehiscent and nut-like; seeds 1–many, generally reniform-round, compressed, the embryo curved, endosperm mealy.

A family of weedy plants composed of 15–25 genera. Only 2 genera are represented in Panama.

a. Leaves estipulate; ovary superior; styles 3; capsule loculicidal, 3-valved, splitting from the apex towards the base..... 1. Talinum
aa. Leaves stipulate or estipulate, the stipules scarious, fimbriate or tufted; ovary half to wholly inferior; styles 1–9; capsule circumscissile..... 2. Portulaca

1. TALINUM Adans.

Talinum Adans. Fam. 2:245. 1763.

Helianthemoides Medik. Phil. Bot. 1:95. 1789.
Phemeranthus Raf. in Med. Repos. N. Y. 5:350. 1808.
Talinium Raf. in Amer. Monthly Mag. 175. 1818.
Litanum Nieuwl. in Amer. Midl. Nat. 4:90. 1915.

Herbs, subshrubs or shrubs, often succulent. Leaves alternate or approximate, terete to plane, fleshy; estipulate. Inflorescence terminal or rarely axillary, paniculiform, cymose or the flowers solitary. Sepals 2, opposite, deciduous or rarely persistent. Petals 5, rarely more, connate at the base or free, deciduous. Stamens 5–30, in antipetalous fascicles. Ovary superior, sessile or short-stipitate, the ovules numerous, the styles 3, more or less united, filiform. Capsule loculicidal, 3-valved, splitting from the apex to the base, chartaceous; seeds reniform-round, numerous, the embryo incompletely annular, the testa smooth, striate or tuberculate, distinctly or indistinctly strophiolate.

A genus of about 50 species of which only 1 is found in Panama.

1. Talinum paniculatum (Jacq.) Gaertn. Fruct. 2:219. 1791.

Portulaca paniculata Jacq. Enum. Pl. Carib. 22. 1760.
Portulaca patens L. Mant. 242. 1771.
Roelingia patens (L.) Ehrh. Beitr. 3:135. 1788.
Talinum reflexum Cav. Ic. 1:1. 1791.
Talinum dichotomum Ruiz & Pav. Syst. Veg. 118. 1798.
Talinum patens (L.) Willd. Sp. Pl. 2:863. 1800.
Portulaca reflexa (Cav.) Haw. Misc. Nat. 141. 1803.
Talinum fruticosum Macfad. Fl. Jam. 2:169. 1850.
Talinum sarmentosum Englm. in Bost. Journ. Nat. Hist. 6:153. 1850.
Talinum spathulatum Englm. in Gray, Pl. Wright. 1:14. 1852.
Talinum purpureum Hort. ex Englm. loc. cit. 1852.

Fig. 135. *Talinum paniculatum*

Talinum moritziana Klotzsch, ex Rohrb. in Mart. Fl. Bras. 14[2]:295. 1872.
Talinum roseum Klotzsch, ex Rohrb. loc. cit. 1872.
Talinum patens var. *sarmentosum* (Englm.) Gray, in Proc. Amer. Acad. 22:275. 1887.
Claytonia patens (L.) O. Ktze. Rev. Gen. 1:56. 1891.
Claytonia paniculata (Jacq.) O. Ktze. loc. cit. 57. 1891.
Claytonia reflexa (Cav.) O. Ktze. loc. cit. 1891.
Claytonia sarmentosa (Englm.) O. Ktze. loc. cit. 1891.
Talinum reflexum f. *sarmentosum* (Englm.) Small, Fl. SE. U. S. 415. 1903.
Talinum chrysanthum Rose & Standl. in Contr. U. S. Nat. Herb. 13:288. 1911.
Talinum paniculatum var. *sarmentosum* (Englm.) v. Poellnitz, in Deut. Bot. Gessel. Berichte 51:123. 1933.

Herbaceous plants, erect, slender, glabrous throughout, the root often thick and fleshy. Leaves alternate, broadly elliptic to obovoid, rarely oblanceolate, 4–13 cm. long, 1.5–5.5 cm. broad, acute to obtuse at the apex, cuneate or attenuate at the base, plane, petiole 3–15 mm. long. Inflorescence terminal, compound, lax, 10–60 cm. long, 6–20 cm. broad, the lateral simple or compound cymes racemosely arranged on the primary rhachis, bracteate; pedicel 6–25 mm. long, dilated distally. Sepals ovate, 1.5–3.0 mm. long and broad, connate at the base, slightly keeled, reflexing and deciduous; petals elliptic, 3.0–4.5 mm. long, about 1 mm. broad; stamens 15 or more, the filaments 1.5–2.0 mm. long, free, the anthers ovoid, to 0.5 mm. long and broad; ovary sessile, globose, about 1 mm. long, 1 mm. in diameter. Capsule ovoid to globose, 3–5 mm. long, 3–5 mm. in diameter; seeds

strongly reniform, 0.75–1.0 mm. in diameter, the testa minutely striate, black, indistinctly strophiolate.

Southern United States, Central and South America, West Indies, southern Asia and the East Indies.

PANAMÁ: Isla Taboga, *Woodson, Allen & Seibert 1491*.

2. PORTULACA L.

PORTULACA L. [Syst. ed. 1. 1735]; Sp. Pl. 445. 1753.

Meridiana L. f. Suppl. 248. 1781.
Lemia Vand. Fl. Lus. & Bras. Sp. 35, *t. 2. f. 15*. 1788.
Merida Neck. Elem. 2:382. 1790.
Portulacca Haw. Synop. 121. 1812.
Lamia Vandelli ex Endl. Gen. 949. 1840.

Annual or perennial herbs, succulent. Leaves alternate or approximate, terete to plane, often whorled about the flowers; stipules scarious, fimbriate or tufted, sometimes very small, rarely absent. Inflorescence near the stem apex, crowded, the flowers sometimes solitary, yellow to red. Sepals 2, opposite, connate below, the anterior larger than the posterior, usually persistent. Petals 4–6, connate at the base or free, somewhat auto-deliquescent. Stamens 4 to many, inserted at the base of the petals, the filaments often hairy below. Ovary half to wholly inferior, the ovules numerous, the styles 3- to 9-parted, rarely simple. Capsule circumscissile, chartaceous; seeds reniform to cochleate, numerous, the testa smooth or minutely tuberculate.

A cosmopolitan genus in tropical and subtropical areas of the world, about 125 species.

1. PORTULACA OLERACEA L. Sp. Pl. 445. 1753.

Portulaca parvifolia Haw. Syn. Pl. Succ. 122. 1812.
Portulaca marginata HBK. Nov. Gen. & Sp. 6:58. 1823.
Portulaca oleracea β *parviflora* (Haw.) Griseb. Fl. Brit. W. Ind. 57. 1864.
Portulaca oleracea α *macrantha* Eggers, Fl. St. Croix 27. 1879.
Portulaca oleracea β *micrantha* Eggers, loc. cit. 1879.

Plants herbaceous, radially spreading and prostrate or somewhat ascending, glabrous throughout, the roots fibrous. Leaves alternate, elliptic to obovoid, 1–3 cm. long, 0.5–1.0 cm. broad, generally obtuse at the apex, cuneate at the base, plane; petiole 1–8 mm. long, the stipules fimbriate, inconspicuous. Inflorescence with the flowers crowded, the flowers sessile or essentially so, yellow. Perianth tube crateriform, 1 mm. long, 1.5 mm. in diameter; sepals ovate, 3.0–4.5 mm. long, 3–4 mm. broad, strongly keeled, connate at the base, generally persistent and enclosing the operculum of the fruit; petals 4, 3.0–4.5 mm. long, 1.5–3.0 mm. broad; stamens 6–15, the filaments 1.5–1.75 mm. long, the anthers globose, to 0.5 mm. long and broad; ovary half-inferior, short-conical, the style lobes 4–6. Capsule ovoid to fusiform, 6–9 mm. long, about 2.5 mm. in diameter, circumscissile

slightly below the middle; seeds almost cochleate, about 0.5–0.75 mm. in diameter, the testa minutely tuberculate, almost black.

Known as *verdolaga* in Panama. According to Standley (Field Mus. Nat. Hist. Bot. 18:429. 1937) the plant is used as a pot herb throughout Central America.

BOCAS DEL TORO: vicinity of Nievecita, *Woodson, Allen & Seibert 1862.* CHIRIQUÍ: Boquete, *Davidson 705.* DARIÉN: vicinity of Boca de Cupe, *Allen 875*; Río Chucunaque, *Leopold 758.* PANAMÁ: San José Island, *Johnston 901.*

Fig. 136. *Portulaca oleracea*

CARYOPHYLLACEAE

By JAMES A. DUKE

Annual or perennial herbs or subshrubs, often with swollen nodes. Leaves opposite and decussate or verticillate, the petioles often amplexicaul, some with conspicuous stipules. Flowers commonly bisexual, actinomorphic, 5- or 4-merous, in dichasial cymes, or solitary in the axils, or solitary and terminal (*Githago*). Sepals 5–4, separate or connate, often scarious, persistent. Petals as many as the sepals, rarely absent, hypogynous or slightly perigynous, entire, bifid or lacerate, usually white, pink or red. Stamens 2–10, mostly 5 or 10; filaments filiform or flattened, occasionally united into a short tube below; anthers usually versatile, 2-celled, and longitudinally dehiscent. Carpels 2–5, the ovary 1-locular, with 1–many campylotropous ovules on basal, central or free central placentae, styles 2–5, free or united below. Fruit a utricle or a capsule longitudinally dehiscing into as many entire or deeply emarginate valves as there are styles; seeds 1–many, strophiolate or estrophiolate, smooth or tuberculate, the embryo curved about the perisperm.

This family, with about 75 genera, mostly in temperate areas, is of little economic interest except for a number of ornamentals, such as *Lychnis* and *Dianthus*, which may ultimately be found in Panama gardens. Several weedy genera, of more or less cosmopolitan distribution, despairingly need monographic research, worldwide in scope. Five such weedy genera occur in Panama.

a. Leaves longer than broad; stipules absent; stamens usually 10, rarely 4 or 5; capsule splitting into 2–5 usually 2-cleft valves; styles not united.
  b. Leaves linear to elliptic; petals entire or shallowly emarginate..... 1. Arenaria
  bb. Leaves ovate to cordate; petals deeply bifid.
    c. Leaves ovate; capsules cylindric, arcuate, with 10 teeth; styles usually 5..... 2. Cerastium
    cc. Leaves ovate or cordate; capsules ovoid, straight, with 6–8 (–10) teeth; styles usually 2–4..... 3. Stellaria
aa. Leaves shorter or longer than broad; stipules present, occasionally fugaceous; stamens 2–5; capsules splitting into 3 entire valves; styles usually united at least half their length.
  d. Leaves broader than long, opposite, the ochraceous stipules often fugaceous; seeds 1–50, tuberculate in lines (in Panama)..... 4. Drymaria
  dd. Leaves longer than broad, verticillate, the argentate stipules persistent; seeds 2–6, merely corrugated..... 5. Polycarpaea

1. ARENARIA L.

Arenaria L. [Rupp. ex L. Syst. ed. 1. 1735] Sp. Pl. 423. 1753.

Moehringia L. [Syst. ed. 2:22. 1740] Sp. Pl. 359. 1753.
Minuartia L. Sp. Pl. 89. 1753
Gypsophytum Adans. Fam. 2:256. 1763.
Ammodenia Patrin, ex Gmel. Fl. Sibir. 4:160. 1769.
Alsine Scop. Fl. Carn. ed. 1:496. 1772. not L. 1753.
Honkenya Ehrh. Beitr. 2:180. 1788.
Leptophyllum Ehrh. loc. cit. 4:147. 1789.

Spergulastrum Michx. Fl. Bor. Am. 1:275. 1803. in part.
Alsinella Swartz, Summa Veg. Scand. 17. 1814.
Gouffeia Robill. & Cast. in Lam. & DC. Fl. Fr. 5:609. 1815.
Halianthus Fries, Fl. Holland 75. 1817.
Adenarium Raf. in Desv. Jour. Phys. 89:249. 1818.
Bigelovia Raf. in Jour. Phys. 89:289. 1819.
Siebera Hoppe, in Flora 2:24. 1819.
Somerauera Hoppe, loc. cit. 2:26. 1819.
Merckia Reichb. ex Cham. & Schlecht. in Linnaea 1:59. 1826.
Brachystemma D. Don, Prodr. Fl. Nep. 216. 1828.
Wilhelmsia Reichb. Consp. 206. 1828.
Odontostemma Benth. in Wall. Cat. *n. 645.* 1828.
Sabulina Reichb. Fl. Germ. Excurs. 785. 1832.
Eremogone Fenzl, Verbr. Alsin. 13:18. 1833.
Chetrophis Raf. Fl. Tell. 3:80. 1836.
Dolophragma Fenzl, in Ann. Wien. Mus. 1:63. *t. 7.* 1836.
Merkia Reichb. Handb. 298. 1837.
Plinthine Reichb. loc. cit. 298. 1837.
Alsinanthus Reichb. loc. cit. 298. 1837.
Dufourea Gren. in Act. Soc. Linn. Bord. 9:25. 1837.
Lepyrodiclis Fenzl, in Endl. Gen. 966. 1840.
Alsinanthe Reichb. Ic. Fl. Germ. 5:29. 1841.
Facchinia Reichb. loc. cit. 5:29. 1841.
Neumayera Reichb. loc. cit. 5:30. 1841.
Pettera Reichb. Nom. 205. 1841.
Tryphane Reichb. loc. cit. 205. 1841.
Wierzbickia Reichb. loc. cit. 205. 1841.
Greniera J. Gay, in Ann. Sci. Nat. 3^4:27. 1845.
Rhodalsine J. Gay, loc. cit. 3^4:25. 1845.
Strophium Dulac. Fl. Hautes-Pyr. 247. 1867.
Xeralsine Fourr. in Ann. Soc. Linn. n. s. 16:347. 1868.
Euthalia Rupr. Fl. Caucas. 220. 1869.
Brewerina A. Gray, in Proc. Am. Acad. 8:620. 1869.
Alsinopsis Small, Fl. S. E. U. S. 419 & 1330. 1903.

Annual, biennial or perennial herbs, glabrous or pubescent, prostrate and cespitose to diffuse and spreading, the stems somewhat resilient and occasionally suffruticose below. Leaves opposite, petiolate to sessile and slightly amplexicaul, exstipulate, subulate and coriaceous to broadly elliptic and membranaceous. Flowers axillary or terminal, solitary or in dichasial cymes. Sepals 5, connate only at the base if at all. Petals 5, rarely lacking, white or occasionally red, entire or shallowly emarginate. Stamens 10, rarely 5; anthers versatile; 2-celled, longitudinally dehiscent; filaments flattened and usually united below to form a slightly perigynous disk. Ovary superior, 3- (2–5-) carpellate with 3 (2–5) filiform styles free to their bases; ovules numerous on basal placentae. Capsule dehiscing into as many entire to deeply emarginate valves as there are styles; seeds numerous, cochleate, smooth to tuberculate, estrophiolate, the embryo curved about the perisperm.

A weedy genus containing nearly 200 species, this nearly cosmopolitan genus is in the tropics largely restricted to high altitudes. Fernald (in Rhodora 21:1. 1919) presents adequate reasons for retaining *Arenaria sensu lato* instead of maintaining several poorly separated generic segregates. Three intergrading units, best treated as subspecies of one polymorphic species, *A. lanuginosa*, are found in Panama.

a. Leaves oblong, lanceolate or ovate, the larger less than 20 mm. long; sepals glabrous or pubescent in lines, 2–5 mm. long, the petals and capsules longer or shorter; plants cespitose or diffuse.
  b. Plants diffuse, loosely spreading; sepals pubescent, 2–4 mm. long, the petals 2–4.5 mm. long; pedicels much longer than the subtending leaves; leaf margins usually plane..... 1. ssp. LANUGINOSA
  bb. Plants cespitose, much branched near the base, some of the branches occasionally proliferating; sepals glabrous, 3–5 mm. long, the petals 4–6 mm. long; pedicels shorter or longer than the subtending leaves; leaf margins usually involute..... 2. ssp. SAXOSA
aa. Leaves lanceolate, the larger over 20 mm. long; sepals conspicuously pubescent on the costae, 4–6 mm. long, the petals and capsules longer; plants diffuse and spreading..... 3. ssp. GUATEMALENSIS

1. ARENARIA LANUGINOSA ssp. LANUGINOSA Maguire, in Am. Midl. Nat. 48:498. 1951.

Spergulastrum lanuginosum Michx. Fl. Am. Bor. 1:275. 1803.
Micropetalum lanuginosum (Michx.) Pers. Syn. Pl. 1:509. 1805.
Arenaria alsinoides Willd. ex Schlecht. in Mag. Gesells. Nat. Freund. Berl. 7:201. 11816.
Stellaria elongata Nutt. Gen. 1:289. 1818.
Arenaria diffusa Ell. Sketch. Bot. S. C. & Ga. 1:519. 1821.
Arenaria nemorosa HBK. Nov. Gen. & Sp. 6:35. 1823.
Arenaria nemorosa α quitensis DC. Prodr. 1:409. 1824.
Arenaria nemorosa β novogranatensis DC. loc. cit. 1:409. 1824.
Arenaria jussiaei Camb. ex St. Hilaire, Fl. Bras. Mer. 2:126. 1829.
Arenaria scabra Vahl, ex St. Hilaire, loc. cit. 2:126. 1829.
Arenaria paradoxa Bart. Rel. Haenk. 2:15. 1831.
Stellaria lanuginosa (Michx.) Torr. & Gray, Fl. Amer. Bor. 1:187. 1840.
Arenaria lanuginosa α genuina Rohrb. in Linnaea 37:260. 1872.
Arennaria lanuginosa β diffusa Rohrb. loc. cit. 37:263. 1872.
Arenaria lanuginosa diffusa (Ell.) Macloskie, Rep. Princeton Univ. Exped. Patag. 8:394. 1905.
Stellaria laxa Muschl. in Bot. Jahrb. 45:443. 1911.
Arenaria lanuginosa var. *longipedunculata* Duncan, in Phytologia 3:282. 1950.

Herbaceous puberulent laxly spreading perennials. Leaves opposite, lanceolate, oblanceolate or narrowly elliptic, apically attenuate and mucronulate, basally subsessile and attenuate, 5–20 mm. long, 2–5 mm. broad, scantily to densely puberulent with a whitish indumentum, often ciliate on the margins. Flowers solitary in the axils, the puberulent pedicels much longer than the subtending leaves. Sepals lanceolate to ovate, attenuate, puberulent 2–4.5 mm. long; petals 5, occasionally absent, obovate, entire, 2–4.5 mm. long; stamens 10, the filaments 1–4 mm. long; ovary sessile or short-stipitate, ovoid; styles 2–4. Capsule ovoid, 3–5 mm. long, the 2–4 valves deeply emarginate; seeds numerous, on basal placentae, cochleate, dark reddish brown to black, smooth or minutely tuberculate, ca. 0.75 mm. broad.

Southeastern U. S. to Peru and Bolivia, in Central America only at moderate elevations.

CHIRIQUÍ: vicinity of "New Switzerland", central valley of Río Chiriquí Viejo, 1800–2000 m., *Allen 1414*; vicinity of Boquete, 1200–1500 m., *Woodson & Schery 802*.

The typical species was originally described as apetalous, as are most specimens from the southeastern United States, the type locality. In Mexico and Central America however, where the ranges of several subspecies overlap, the large majority

of specimens, obviously referable to this "apetalous" subspecies, have petals nearly or quite as long as the sepals.

MacBride (in Field Mus. Bot. 13[2]:601. 1936–8) reports that in Peru, where the plant is called *celedonia* and *tauchchalli*, it is the source of an astringent used for hemorrhages of the uterus.

2. ARENARIA LANUGINOSA ssp. SAXOSA (A. Gray) Maguire, in Am. Midl. Nat. 48: 498. 1951.

Arenaria saxosa A. Gray, Pl. Wright. 11:18. 1853.
Arenaria saxosa var. *cinerascens* Robinson, in Proc. Am. Acad. 29:293. 1894.
Arenaria confusa Rydb. in Bull. Torr. Club 28:275. 1901.
Arenaria polycaulos Rydb. loc. cit. 31:406. 1904.
Arenaria mearnsii Woot. & Standl. in Contr. U. S. Nat. Herb. 16:121. 1939.
Arenaria saxosa var. *mearnsii* (Woot. & Standl.) Kearney, & Peebles, in Jour. Wash. Acad. 29:475. 1939.

Herbaceous (occasionally subligneous at the base) puberulent cespitose perennials, some of the branches occasionally proliferating and spreading. Leaves opposite, mostly linear-lanceolate, apically attenuate and mucronulate, basally subsessile and rounded to acute, 5–18 mm. long, 1–3 mm. broad, scantily to densely puberulent with a whitish indumentum, often ciliate on the involute margins. Flowers solitary in the axils, the puberulent pedicels longer or occasionally shorter than the subtending leaves. Sepals lanceolate to ovate, attenuate, glabrous, 3–5 mm. long; petals 5, obovate, entire, 4–6 mm. long; stamens 10, the filaments 1–4 mm. long; ovary sessile or short-stipitate, ovoid; styles 2–4. Capsule ovoid, 3–5 mm. long, the 2–4 valves deeply emarginate; seeds numerous, on basal placentae, cochleate, dark reddish brown, usually tuberculate, ca. 0.75 mm. broad.

Southwestern U. S. to Mexico; Panama to northwestern South America, at rather high elevations.

CHIRIQUÍ: Potrero Muleto, Volcán Chiriquí, Boquete District, 10,400 ft., *Davidson 1041 & 1051*; Potrero Muleto to summit, Volcán Chiriquí, 3500–4000 m., *Woodson & Schery 405 & 434*; Loma Larga to summit, Volcán Chiriquí, 2500–3380 m., *Woodson, Allen & Seibert 1073*.

3. ARENARIA LANUGINOSA ssp. **guatemalensis** (Standl. & Steyerm.) J. Duke comb. & stat. nov.

Arenaria guatemalensis Standl. & Steyerm. in Field Mus. Bot. 23:50. 1944.

Herbaceous puberulent laxly spreading perennials. Leaves opposite, lanceolate, apically attenuate and mucronulate, basally subsessile and attenuate, 10–40 mm. long, 2–6 mm. broad, irregularly puberulent with a whitish indumentum, often ciliate on the margins. Flowers solitary in the axils, the puberulent ebracteate pedicels 10–40 mm. long, usually exceeding the subtending leaves. Sepals lanceolate to ovate, attenuate, strongly puberulent on the costa, 4–6 mm. long; petals 5, obovate, entire, 5–8 mm. long; stamens 10, the filaments 3–6 mm. long; ovary sessile or short-stipitate, globose or ovoid; styles 2–4. Capsule ovoid, 5–8 mm. long, the 3 valves deeply emarginate; seeds numerous, on basal placentae, cochleate,

Fig. 137. *Arenaria lanuginosa* ssp. *guatemalensis*

dark reddish brown to black, smooth or minutely tuberculate, ca. 0.75 mm. broad.

Mexico to Panama, at moderate elevations.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, 6000 ft., *Davidson 256*; vicinity of Finca Lérida, 1750 m., *Woodson & Schery 214*; vicinity of Casita Alta, Volcán Chiriquí, ca. 1500–2000 m., *Woodson, Allen & Seibert 819*; valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, 1300–1900 m., *Seibert 297*; in grassy sunny places, vicinity of Cerro Punta, 1500–2000 m., *Seibert 260*.

Other variants of the *lanuginosa* complex are found in Mexico and Central America and could conceivably occur in Panama. In the subspecies *guatemalensis*, the variety *ensifolia*, with linear leaves and exerted petals, is so far reported only from southern Mexico. Characterized by ovate leaves, cuneate to cordate leaf bases and exerted petals, the variant currently passing as *A. megalantha* (Rohrb.)

F. N. Williams would probably better be treated as a *lanuginosa* subspecies, ranging from southern Mexico to Guatemala. The original description of *A. guatemalensis* would have been more edifying had it been contrasted with *A. lanuginosa* instead of *A. megalantha*, for although intergrades occur between all three, they are more frequent and perplexing between the first two. The relative constancy of these three taxa, where their ranges are distinct, coupled with limited intergradations near the commissures of their ranges, seems to justify their relegation to the subspecific level, in accord with the heirarchy established by Maguire (in Am. Midl. Nat. 46:493. 1951) in his monograph of the North American species of *Arenaria*.

2. CERASTIUM L.

CERASTIUM L. Sp. Pl. 437. 1753.

Prevotia Adans. Fam. 2:256. 1763.
Centunculus Adans. loc. cit. 2:256. 1763.
Moenchia Ehrh. Beitr. 2:177. 1788.
Quaternella Ehrh. loc. cit. 4:149. 1789.
Doerriena Borkh. in Rhein Mag. 1:528. 1793.
Myosotis Tourn. ex Moench, Meth. 224. 1794.
Esmarchia Reichb. Fl. Germ. Excurs. 793. 1832.
Doerriera Steud. Nom. 2^1:522. 1840.
Prevoita Steud. loc. cit. 394. 1840.
Pentaple Reichb. Ic. Fl. Germ. 5:37. *t. 227*. 1841.
Dichodon Bartl. ex Reichb. Nom. 205. 1841.
Leucodonium Opiz, Seznam 59. 1852.

Annual or perennial, usually pubescent, erect or decumbent herbs. Leaves opposite, usually sessile or subsessile, exstipulate, often viscid. Flowers few in dichasial cymes, white. Sepals 5, rarely 4, not connate. Petals as many as the sepals, rarely absent, emarginate or 2-cleft, white. Stamens 10, occasionally less; anthers versatile, 2-celled, longitudinally dehiscent; filaments flattened, scarcely if at all connate to form an obscurely glandular annulus. Ovary superior; carpels 5, rarely fewer, with as many distinct styles, the many campylotropous ovules arising from basal or central placentae. Capsule often arcuate (hence the generic name), dehiscing longitudinally into as many deeply emarginate valves as there are styles; seeds numerous, cochleate, usually tuberculate, estrophiolate, the embryo coiled about the perisperm.

Of this weedy cosmopolitan, temperate genus, only one of about fifty species occurs in Panama.

1. CERASTIUM VISCOSUM L. Sp. Pl. 437. 1753.

Cerastium glomeratum Thuill. Fl. Paris 225. 1799.
Cerastium consanguineum Wedd. in Ann. Sci. Nat. 5^1:296. 1864.
Cerastium viscosum β consanguineum (Wedd.) Rohrb. in Linnaea 37:284. 1872.

Herbaceous viscid-villous freely branching annuals, prostrate, spreading or erect. Leaves opposite, viscid-villous, elliptic to ovate or obovate, apically rounded

Fig. 138. *Cerastium viscosum*

and usually mucronulate, basally attenuate, 5–25 mm. long, 3–15 mm. broad, the winged petioles less than 5 mm. long. Flowers few in terminal dichasial cymes with reduced foliaceous bracts at the major dichotomies, the lanate to villous pedicels becoming 5–10 mm. long, exceeding the subtending bracts. Sepals 5, ovate to lance-oblong, acute to attenuate, villous, 3–5 mm. long; petals 5, rarely none, oblong, deeply 2-cleft, 3–5.5 mm. long; stamens 10, the flattened filaments 2–4 mm. long; ovary sessile or short-stipitate, ovoid; styles usually 5, 1.5–2 mm. long, glandular throughout; ovules many, campylotropous on central placentae. Capsule subcylindric, arcuate, 6–8 mm. long, the 5 valves deeply 2-cleft; seeds numerous, cochleate, light brown, minutely tuberculate, ca. 1 mm. broad.

Naturalized from Europe, now rather common throughout temperate and tropical America.

CHIRIQUÍ: Potrero Muleto to summit, Volcán Chiriquí, 3500–4000 m., *Woodson & Schery 472*; vicinity of Boquete, 1200–1500 m., *Woodson & Schery 804*.

3. STELLARIA L.

STELLARIA L. Sp. Pl. 421. 1753.

Myosoton Moench. Meth. 225. 1794.
Spergulastrum Michx. Fl. Am. Bor. 1:275. 1803. In part.

Micropetalon Pers. Syn. 1:509. 1805.
Alsinella Swartz, Summa Veg. Scand. 17. 1814. In part.
Larbrea St. Hilaire, in Mém. Mus. Par. 2:287. 1815.
Malachium Fries, Fl. Halland. 77. 1817.
Ballarion Raf. in Am. Month. Mag. 266. 1818.
Leucostemma Benth. in Wall. Cat. *n. 642*. 1828.
Krascheninikovia Turcz. ex Bess. in Flora 17[1] Beibl.: 9. 1834.
Adenonema Bunge, in Mem. Sav. Etr. Petersb. 2:448. 1836.
Schizotechium Reichb. Nom. 205. 1841.
Hylebia Fourr. in Ann. Soc. Linn. Lyon n. s. 16:347. 1868.
Myosanthus Fourr. loc. cit. n. s. 16:348. 1868.

Annual or perennial herbs, often much branched and clambering, the stems somewhat resilient and occasionally suffruticose below. Leaves opposite, petiolate or sessile and somewhat perfoliate, exstipulate, in Central America rather broad and membranaceous. Flowers in few-flowered dichasial cymes or less frequently solitary in the axils of slightly reduced leaves. Sepals 4–5, not connate. Petals 4–5, rarely absent, white, deeply 2-cleft. Stamens 4–10; anthers versatile, 2-celled, the flattened hypogynous filaments connate below forming a brief glandular disk. Ovary superior, carpels 2–4, with as many filiform styles free to the base; ovules 4–many, campylotropous on basal, central or free central placentae. Capsule deeply or shallowly dehiscing into as many 2-cleft or rarely entire valves as there are styles; seeds 4–many, cochleate, smooth or tuberculate, estrophiolate, the embryo curved about the perisperm.

Composed of about a hundred species, this weedy genus is nearly cosmopolitan, but is, as are most caryophyllaceous genera, largely restricted to high altitudes in the tropics. Three of the six Central American species are found in Panama.

a. Flowers solitary in the axils or in few-flowered leafy cymes; sepals and petals 5; stamens 8–10; seeds numerous; pedicels not glandular-villous; leaves ovate or cordate.
  b. Leaves cordate; petals 8–10 mm. long, 1.5–2 times as long as the sepals; spines on the seeds usually broader than long..... 1. S. NEMORUM
  bb. Leaves ovate; petals 3–6 mm. long, 1–1.5 times as long as the sepals; spines on the seeds usually longer than broad..... 2. S. OVATA
aa. Flowers many in dichasial cymes with minute bracts; sepals and petals 4; stamens 4–6 (–8); seeds 4–6; pedicels glandular-villous, leaves cordate. 3. S. IRAZUENSIS

1. STELLARIA NEMORUM L. Sp. Pl. 421. 1753.

Cerastium nemorum Crantz, Inst. 2:401. 1766.
Stellaria nemoralis Salisb. Prodr. 301. 1796.
Stellaria cuspidata Willd. ex Schlecht. in Ges. Natur. Freund. Berlin Mag. 7:196. 1816.
Stellaria reichenbachii Wierzb. in Reichb. Ic. Fl. Germ. 5:34. 1841.
Stellaria baldwini Fenzl, in Linnaea 30:57. 1859-60.
Stellaria ciliata β cuspidata (Willd.) Rohrb. in Linnaea 37:278. 1872.
Stellaria nemorum var. *japonica* Franch. & Sav. Enum. Pl. Jap. 2[1]:295. 1876.
Stellaria montana Pierrat, in Soc. Bot. Roche 2:58. 1880.
Stellaria nemorum subsp. *glochidosperma* Murb. in Act. Univ. Lunds. 27:156. 1892.
Stellaria nemorum subsp. *montana* (Pierrat) Murb. Bot. Notiser 201. 1899.
Stellaria nemorum subsp. *montana* forma *reichenbachii* (Wierzb.) Murb. loc. cit. 201. 1899.
Stellaria francheti Honda, in Bot. Mag. Tokyo 43:541. 1929.
Stellaria limitanea Standl. in Field Mus. Bot. 22:74. 1940.

Herbaceous glabrous to pubescent profusely branching perennials, prostrate,

spreading or clambering. Leaves opposite, glabrous to viscid-villous, ovate, apically acute to attenuate, basally truncate to cordate, 10–50 mm. long, 5–35 mm. broad, all except the uppermost petiolate, the petioles 5–40 mm. long. Flowers solitary, axillary or terminal, or in terminal few-flowered cymes, the glabrous to villous pedicels 5–45 mm. long, often exceeding the subtending leaves. Sepals 5, lanceolate to ovate, acute to attenuate, glabrous to villous, 4–6 mm. long; petals 5, obovoid, deeply 2-cleft, 6–12 mm. long; stamens 10, the filaments flattened, 3–8 mm. long; ovary sessile, globose to ovoid; styles usually 3, 2–3 mm. long, the numerous ovules campylotropous on basal or free central placentae. Capsule ovoid, 4–7 mm. long, the 3 valves deeply 2-cleft; seeds numerous, ca. 1 mm. broad, cochleate, dark reddish brown, tuberculate, the spines usually broader than long.

In the New World, extending from Mexico to Patagonia.

BOCAS DEL TORO: Robalo trail, northern slopes of Cerro Horqueta, 6000–7000 ft., *Allen 4997*. CHIRIQUÍ: Potrero Muleto to summit, Volcán Chiriquí, 3500–4000 m., *Woodson & Schery 393*.

The New World material seems indistinguishable from the Old World material except that seeds tend to be more uniformly tuberculate and leaves do not tend to be so large in New World specimens. Phytogeographically it might seem that New World specimens might at least deserve subspecific rank, but I am unable to detect any constant differentia therein. The non-papillate tubercles on the seeds of Panama representatives more closely resemble those of the European subspecies *montana* (Pierrat) Murb. than those of the subspecies *glochidosperma* Murb.

2. STELLARIA OVATA Willd. ex Schlecht. in Ges. Naturf. Freund. Berl. Mag. 7:196. 1816.

Herbaceous mostly glabrous, branching perennials, prostrate or spreading. Leaves opposite, glabrous or subglabrous, ovate to broadly ovate, apically rounded and mucronulate, basally rounded but slightly attenuate, 10–40 mm. long, 5–30 mm. broad, the petioles 3–8 mm. long. Flowers solitary in the axils, the glabrous to villous pedicels 10–40 mm. long, usually exceeding the subtending leaves. Sepals 5, ovate to obovate, obtuse to acute, glabrous to villous, 2.5–5 mm. long; petals 5, obovate, deeply 2-cleft, 3–6 mm. long; stamens 10, the flattened filaments 3–4.5 mm. long; ovary sessile, ovoid; styles usually 3, 1–1.5 mm. long, the numerous ovules campylotropous on basal placentae. Capsule ovoid, 3–5 mm. long, the 3 valves deeply 2-cleft, occasionally entire; seeds numerous, ca. 1 mm. broad, cochleate, dark reddish brown, tuberculate, the mature spines usually longer than broad.

Mexico through Central America to northern and western South America.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, 1300–1900 m., *White & White 3*; valley of the upper Río Chiriquí, vicinity of Monte Lirio, 1300–1900 m., *Seibert 275*; Palo Alto, just e. of Boquete, 5000 ft., *Stern, Chambers et al. 1007*.

Standley and Steyermark (in Field Mus. Bot. 24[4]:238. 1946) report the following vernacular names are applied in Guatemala: *tripa de pollo, culantro de monte* and *cuartillera*.

Fig. 139. *Stellaria irazuensis*

3. Stellaria irazuensis Donn. Smith, in Bot. Gaz. 23:236. 1897.

Herbaceous, mostly glabrous, much branching perennials, prostrate or spreading. Leaves glabrous, ovate to deltoid, apically attenuate, basally cordate, 10–20 mm. long, 5–15 mm. broad, the scantily villous petioles 5–15 mm. long. Flowers several in dichotomously branching cymes 10–25 cm. long, with minute bracts at the major dichotomies, the glandular-villous pedicels 5–10 mm. long. Sepals 4, narrowly ovate to elliptic, obtuse to acute, glabrous or glabrate, 1.5–2.5 mm. long; petals 4, deeply 2-cleft, the segments linear, 1.5–3.0 mm. long; stamens 4–6 (–8), the flattened filaments 1.5–2.5 mm. long; ovary sessile, ellipsoid; styles usually 2, ca. 1 mm. long, the 4–6 ovules campylotropous on basal placentae. Capsule flattened, ellipsoid, ca. 2 mm. long, the 2 valves emarginate; seeds 6 or less, ca. 1 mm. broad, cochleate, dark reddish brown, tuberculate.

Guatemala to Panama.

chiriquí: vicinity of Bajo Chorro, 1900 m., *Woodson & Schery 640*.

Further study of this distinctive tetramerous species may well prove it to be conspecific with S. *venezuelana* Steyerm., which Steyermark rightly separated from the heterogeneous assemblage described as S. *micrantha* Spruce ex Rohrb. Rohrbach's description is not at all applicable to *Fendler 47* which was designated as cotype of S. *micrantha*, and which is quite apparently referable to S. *venezuelana*.

4. DRYMARIA Willd. ex Roem. & Schult.

Drymaria Willd. ex Roem. & Schult. Syst. 5:31. 1819.
Pinosia Urban, in Arkiv Bot. 23A[5]:70. *pl. 2.* 1930.
Mollugophytum M. E. Jones, in Extr. Contr. West. Bot. 18:35. 1933.

Annual or perennial, glabrous to pubescent herbs, occasionally subligneous below, prostrate, spreading or erect. Leaves opposite, with persistent or fugaceous small stipules, sessile or petiolate, glabrous to villose, the hairs often glandular. Flowers in few-flowered racemes or in dichasial cymes, rarely solitary in the axils. Sepals 5, not connate. Petals (0–) 5, white, usually 2-cleft, with the sinus of the cleft occasionally laciniate. Stamens 2–5, the anthers versatile, 2-celled, the flattened filaments slightly connate at the base, rarely with prominent staminodia. Ovary superior, slightly stipitate; carpels 3, the 3 styles united below; ovules few–many, campylotropous on free central placentae. Capsule ovoid to spheroid, dehiscing into 3 entire valves; seeds 1–many, cochleate, foetiform or hippocrepiform, usually tuberculate, the embryo curved about the perisperm.

Exceptional for the Caryophyllaceae in being an almost exclusively tropical genus, *Drymaria* is represented in Panama by only two species. *D. glandulosa* Presl. and *D. palustris*, both ranging from North to South America, have not yet been collected in Panama. The genus consists of perhaps sixty species, all but three confined to tropical and subtropical America. A peculiar group of species with foetiform seeds centers about *D. holosteoides* Benth. which is a seriously toxic range plant of the Sonoran Desert (Little, in Ecology 18:416. 1937). In the only

existing revisionary treatment of the genus, Wiggins (in Proc. Calif. Acad. Sci. 4[25]:189. 1944), dealing with species on and near the Sonoran Desert, recognizes that the seeds are distinctive but lays little emphasis thereon. In my soon forthcoming revision of the whole genus, the seeds are one of the most important diagnostic characters, and the petal and leaf shapes are next respectively in importance to an understanding of the relationships that exist in the genus.

a. Leaves and pedicels scantily to densely villose with long, spreading non-glandular hairs; lobes of the petals acute to emarginate, 2–4-nerved, basally provided with linear auricles; seeds 0.5–0.9 mm. broad, with stellate tubercles..... 1. D. VILLOSA

aa. Leaves glabrous or puberulent; pedicels locally girdled with dense bands of glandular pubescence; lobes of the petals acute, 1-nerved, basally exauriculate; seeds 1.0–1.5 mm. broad, with domical tubercles..... 2. D. CORDATA

1. DRYMARIA VILLOSA Cham. & Schlecht. in Linnaea 5:232. 1830.

Drymaria hirsuta Bartl. in Presl, Rel. Haenk. 2:8. 1831.
Drymaria cubensis Regel, in Otto & Dietr. Allg. Garten. 8:298. 1840.

Fig. 140. *Drymaria villosa*

Drymaria cordata var. *pilosa* Schlecht. in Linnaea 26:374. 1853.
Drymaria cordata var. δ *villosa* (Cham. & Schlecht.) Rohrb. in Mart. Fl. Bras. 14^2:260. 1872.
Drymaria stylosa Backer, in Bull. Jard. Bot. Buitenz. 2^{12}:15. 1913.
Drymaria tepicana M. E. Jones, in Contr. West. Bot. 15:124. 1929.
Drymaria barrancae M. E. Jones, loc. cit. 18:65. 1931.

Prostrate or ascending herbaceous annuals to as much as 45 cm. long, the internodes mostly longer than the leaves, villose to hirsute with septate hairs to as much as 2 mm. long. Leaves opposite, scantily to densely villose or hirsute with cinereous or ochraceous hairs, orbicular to reniform, apically rounded to acute and apiculate, basally cordate to truncate, weakly 3–7-veined, 5–15 mm. long, 5–15 mm. broad; petioles 1–10 mm. long, the stipules mostly entire, scarcely distinguishable from the villosity, 0.5–1.5 mm. long. Inflorescences of terminal 5–many-flowered cymes, the ultimate branches often tending to be racemose; peduncles 1–5 cm. long; bracts 0.5–1.5 mm. long, the pedicels 2–20 mm. long, villose. Sepals 5, 2–3.6 mm. long, 1–2 mm. broad, narrowly to broadly ovate or elliptic, apically acute to obtuse, villose to glabrous, weakly 3-nerved, with translucent borders; petals 5 (absent or drastically reduced in forms passing as *D. tepicana*), 2–3.6 mm. long, bifid for half their length or more, the lobes apically acute to deeply emarginate, 2–4-nerved, basally provided with linear auricles, these very variable in number and orientation; stamens usually 5, 2–3.5 mm. long, the oblong anthers 0.3–0.5 mm. long, the filaments shallowly connate, devoid of staminodia; ovary at anthesis ovoid to globose; styles 3, united for half their length or more, 1–1.5 mm. long; ovules numerous, campylotropous on free central placentae. Capsule ovoid to ellipsoid, 2–3.5 mm. long, many-seeded (rarely as few as two in *D. tepicana*), the seeds cochleate, 0.5–0.9 mm. broad, the dorsal tubercles filiform to capitate or subpinnate, longer than broad, the facial tubercles stellate.

Central Mexico through Central America along the western coast of South America to Peru; apparently introduced and widespread in the East Indies.

CHIRIQUÍ: Finca Lérida to Boquete, ca. 1300–1700 m., *Woodson, Allen & Seibert 1162*; Bajo Chorro, Boquete District, 6000 ft., *Davidson 294*; vicinity of Boquete, 1200–1500 m., *Woodson & Schery 710*. COCLÉ: lower portion of valley and marshes along R. Antón, El Valle de Antón, ca. 500 m., *Hunter & Allen 379*; between Las Margaritas and El Valle, *Woodson, Allen & Seibert 1771*.

Examination of adequate material from Mexico, home of *D. villosa*, from Peru, home of *D. hirsuta*, and Java, home of *D. stylosa*, clearly shows these are conspecific, closely resembling the horticulturally propagated type of *D. villosa*, with the petal lobes spatulate, retuse and basally provided with downwardly directed linear auricles. The Indonesian material is marked, although inconstantly, by glabrous sepals and stiff erect hairs, i. e. they are truly hirsute as contrasted with the predominantly villose Mexican specimens. I have seen no specimens representing this species from the West Indies and believe that the epithet *cubensis* stems from some error in transposition of labels.

Forms comparable to *D. tepicana* M. E. Jones are not infrequent. In these, the petals are reduced to mere vestiges or are completely absent, and the seeds are often fewer in a capsule than is typical, but I am strongly inclined to doubt that these forms warrant even formal recognition. It may be here appropriately mentioned that similar reductions in the petals occur in the closely related species *Drymaria palustris* Cham. & Schlecht., and such variants have been described as *Drymaria townsendii* Robinson.

Standley and Steyermark (in Field Mus. Bot. 24^4:232. 1946) list *poleo, millón* and *llovizna blanca* as Guatemalan names for this species.

2. DRYMARIA CORDATA (L.) Willd. ex Roem. & Schult. Syst. Veg. 5:406. 1819.

Holosteum cordatum L. Sp. Pl. 88. 1753.
Holosteum diandrum Sw. Prodr. 27. 1788.
Drymaria diandra (Sw.) Macfadyen Fl. Jam. 1:52. 1837. non Blume, 1825.
Drymaria cordata β diandra (Sw.) Griseb. Fl. Brit. W. Ind. 56. 1859.
Drymaria cordata β puberula Tr. & Planch. in Ann. Sci. Nat. 4^{17}:148. 1862.
Drymaria procumbens N. E. Rose, in Contr. U. S. Nat. Herb. 1:304. 1895.
Drymaria adenophora Urban, in Fedde, Repert. Sp. Nov. 21:213. 1925.
Drymaria cordata var. *pacifica* Mizushima, in Jour. Jap. Bot. 32:78. 1957.

Glandular-puberulent to glabrate ramifying annuals, prostrate and spreading or erect, the internodes mostly longer than the nodes, glabrous to densely glandular, often rooting at the nodes. Leaves glabrous to scantily pubescent, orbiculate to reniform, apically rounded and occasionally mucronulate, basally rounded to cordate, 5–25 mm. long, 5–30 mm. broad, the petioles 2–15 mm. long; stipules mostly polylacerate, rather persistent, to 2 mm. long. Inflorescences of terminal or axillary few–many-flowered dichasial cymes (flowers rarely solitary in the axils), the bracteate pedicels locally girdled with a dense band of glandular pubescence, rarely subglabrous, 2–15 mm. long, equaling to much exceeding the subtending bracts. Sepals 5, lanceolate to ovate, acute, glandular-puberulent to glabrous, obscurely to strongly 3-nerved, 2.5–4 mm. long, the borders translucent; petals 5, 2–3 mm. long, deeply bifid, the lobes linear, acute, rarely obtuse, 1-nerved, basally exauriculate but rarely subdentate; stamens 2–3 (–5), the flattened filaments 2–2.5 mm. long, the anthers suborbicular, 0.2–0.3 mm. long; styles 3, free nearly to their bases or united for half their length, 0.5–1 mm. long; ovules few to many, campylotropous on free central placentae. Capsule ovoid, 1.5–2.5 mm. long, the 3 valves entire; seeds 1–12, 1.0–1.5 mm. broad, cochleate, dark reddish brown, tuberculate in lines, all the tubercles low and domical, closely approximated or contiguous.

A nearly pantropical species, in America ranging from Florida and Mexico through the West Indies and Central America along both coasts of South America to Argentina.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1249A*. CANAL ZONE: Chagres, Isthmus of Panamá, *Fendler 9*.

Fendler 9 was cited in the original description of *D. cordata β puberula* Tr. & Planch. but differs little, if any, from typical *cordata*. Mizushima (in Jour. Jap.

Bot. 32:69. 1957), studying the varietal potentials of this polymorphic species, described var. *pacifica*, which differs from typical *cordata* in having glabrous sepals, more seeds, and a tendency to have a greater number of stamens and the styles divided completely to the ovary. This rather striking variety seems to be lacking in continental North America. Occurring in both var. *pacifica* and var. *puberula*, for those who wish to recognize them, are variants in which the flowers are subsolitary in the axils. Surprisingly and fittingly these have as yet received no taxonomic status. *Drymaria adenophora* Urban represents a form with diminutive leaves and flowers and apparently is to be expected throughout the range of the species.

Mizushima resurrected *D. diandra* Blume from a long submergence in the synonymy of *D. cordata*. *D. diandra* seems to be confined to the Old World and differs in having pyriform flowers with the outer sepals strongly carinate and three-ribbed, the ribs interconnected. The petal lobes are broader and more obtuse and the seeds tend to be fewer and larger than in *D. cordata*.

Among the many colloquial Central American names for this species reported by Standley and Steyermark (in Field Mus. Bot. 24^4:228. 1946) are *palitaria* or *pelitaria, petatillo, comida de canario, trencilla, comapa, compona* and *nervillo*. Because of its lush mat-forming properties, the plant is often cultivated as a ground cover. According to Dickson (in Tea Quarterly 18:84. 1960) however, the beneficial effects are nullified after a few years, the plant becoming so aggressive as to notably reduce the yield of a tea plantation.

5. POLYCARPAEA Lam.

POLYCARPAEA Lam. in Jour. Hist. Nat. Paris 2:8. *t. 25*. 1792. *Nomen conservandum*.

Anthyllis Adans. Fam. 2:271. 1763. In part.
Polia Lour. Fl. Cochinch. 164. 1790. *Nomen rejiciendum*.
Policarpaea Lam. in Jour. Hist. Nat. Paris 2:1. 1792.
Polycarpoea Lam. loc. cit. 25. 1792.
Hagaea Vent. Tabl. 3:240. 1799.
Hagea Pers. Syn. 1:262. 1805.
Mollia Willd. Hort. Berol. 11. *t. II*. 1806.
Lahaya Roem. & Schult. Syst. 5:402. 1819.
Aylmeria Mart. in Nov. Act. Nat. Cur. 13:276. 1826.
Hyala L'Herit ex DC. Prodr. 3:375. 1828.
Polycarpia Webb, ex Berthel. Hist. Nat. Isles Canary 3^2:156. 1836–50.
Planchonia J. Gay, ex Benth. & Hook. f. Gen. 1:154. 1862.
Robbairea Boiss. Fl. Orient. 1:735. 1867.
Polycarpea Pomel, Nouv. Mat. Fl. Atl. 202. 1874.
Polycarpus O. Ktze. in Post, & O. Ktze. Lexicon 453. 1904. In part.

Annual or perennial, usually pubescent, erect or prostrate herbs. Leaves opposite or verticillate, usually linear and sessile at the swollen nodes, with conspicuous scarious stipules. Flowers in terminal dichasial cymes, white or reddish. Sepals 4–5, occasionally biseriate. Petals 4–5, shorter than the sepals, entire or toothed. Stamens 4–5, the anthers versatile, the flattened hypogynous filaments

Fig. 141. *Polycarpaea corymbosa*

slightly connate below. Ovary superior, unilocular, carpels usually 3; styles united below, the stigmata subcapitate; ovules few, campylotropous on basal placentae. Capsule ovoid to ellipsoid, dehiscing longitudinally into 2–3 entire valves; seeds 1–few, cochleate, tuberculate, the embryo curved about the perisperm.

Primarily a tropical genus of some thirty species, with only one American species reaching as far north as Panama.

1. POLYCARPAEA CORYMBOSA (L.) Lam. Illustr. Gen. 2:129. 1793.

Achyranthes corymbosa L. Sp. Pl. 205. 1753.
Polycarpaea spadicea Lam. Illustr. Gen. 2:129. 1793.
Polycarpaea indica Lam. Encycl. 5:483. 1804.
Mollia spadicea Willd. Hort. Berol. 11. 1816.
Lahaya corymbosa Roem. & Schult. Syst. 5:404. 1819.
Polycarpaea densiflora Wall. Cat. *n. 1513*. 1828.
Polycarpaea brasilensis Camb. in St. Hilaire, Fl. Bras. 2:132. 1829.
Polycarpaea brasilensis var. *β ramosissima* Camb. in St. Hilaire, loc. cit. 2:132. 1829.
Polycarpaea subulata Wight, & Arn. Prodr. 358. 1834.
Polycarpaea atherophora Steud. in Flora 26:763. 1843.
Polycarpaea brevifolia Muell. in Rep. Babb. Exped. 9. 1858.
Polycarpa corymbosa O. Ktze. Rev. Gen. 1:51. 1891.
Polycarpa brevifolia O. Ktze. loc. cit. 1:51. 1891.
Polycarpaea filifolia Muschl. in Bot. Jahrb. 45:453. 1911.
Polycarpaea corymbosa var. *typica* Domin, in Biblioth. Bot. Heft 89^2:655. 1925.
Polycarpaea corymbosa var. *brevifolia* Domin, loc. cit. 89^2:655. 1925.

Herbaceous, argentate-pubescent, erect virgate or tufted annuals or perennials to 1 m. high. Leaves verticillate, linear, aristate, 3–15 mm. long, mostly less than 1 mm. broad, villous or glabrate, the aristate, often lacerate, argentate stipules 2–5 mm. long. Flowers many in congested dichasial cymes, the puberulent pedicels 2–5 mm. long, mostly exceeded by the subtending bracts. Sepals usually 5, occasionally biseriate, lanceolate to ovate, attenuate to aristate, argentate or rarely rufous, often with a darker triangle at the base, 2–4 mm. long; petals 5, obovate, apically undulate, drying yellowish or brown, 0.5–1 mm. long; stamens 5, the flattened filaments 0.5–1 mm. long; ovary short-stipitate, obovoid, the style 0.25–0.50 mm. long, the stigmata minute. Capsule ellipsoid, 1–2.5 mm. long, dehiscing longitudinally into 3 entire valves; seeds 2–6, ca. 0.5 mm. broad, cochleate, minutely corrugated, light brown, on basal placentae.

Usually in arenaceous savannas, cosmopolitan in the tropics, in the Americas reaching its northern limits in Panama.

COCLÉ: in savannas near sea level, Aguadulce, *Pittier 4953*.

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MORPHOLOGY AND ANATOMY OF THE SAURURACEAE. I. FLORAL ANATOMY AND EMBRYOLOGY[1]

M. V. S. RAJU

ABSTRACT

The present paper deals with certain aspects of morphology and anatomy of the Saururaceae. Floral anatomy and embryology suggest a close relationship among the genera. In floral anatomy the genus *Saururus* is the least specialized and *Anemopsis* the most highly specialized. Structure and morphology of inflorescence and also flower suggest the manifestation of certain evolutionary trends, probably guided by reduction, cohesion and adnation. Origin of inferior ovary in the Saururaceae is discussed. Carpels and nature of placentation show certain primitive features. Origin and evolution from apocarpous condition to syncarpous condition of carpels are briefly discussed. Further details will be presented in a separate paper. M. V. S. RAJU, Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

INTRODUCTION

The Saururaceae has been one of the long-neglected angiosperm families in the field of morphology and anatomy. A perusal of the literature shows that earlier investigations have been superficial. In several discussions of comparative morphology and anatomy of the families of the order Piperales and other allied orders, some of the old descriptions of the Saururaceae have been considered. Very often, the family Saururaceae and its composition and affinities have been discussed without much detailed work. In view of this lack of sufficient information, an attempt has been made to investigate in detail some of the salient morphological and anatomical features.

The Saururaceae, according to present knowledge, consists of 6 species—*Saururus cernuus* L., *S. chinensis* (Lour) Baill., *Houttuynia cordata* Thunb., *Anemopsis californica* Hook. & Arn., *Gymnotheca chinensis* Decaisne., and *G. involucrata* P'ei. No material of the last genus was available for this investigation. However, at various stages of description and discussion, previous reports on *Gymnotheca* have been taken into consideration. The present paper deals with floral anatomy and embryology and other related features of the Saururaceae.

Members of the family Saururaceae are perennial aromatic herbs inhabiting moist places. The spirally arranged simple leaves are stipulate (Figs. 1, 5, 8). In *Houttuynia* the stipules are prominent, often enclosing a part of the internode

[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

above the node (Fig. 8). In the other genera, they are not prominently visible but are adnate to the petiole and form a sheath around the node as in monocots. The leaves of *Saururus, Gymnotheca* and *Houttuynia* are auriculate to lanceolate and palmately net-veined. In the case of *Anemopsis*, leaves are elliptic-oblong with a conspicuous mid-vein.

Inflorescence

The inflorescence of the Saururaceae is either a terminal spike or a raceme (Figs. 1, 5, 8). In *Saururus* the naked bracteate flowers are often arranged in pairs, a feature which distorts their spiral arrangement. The flowers are adnate to the subtending bract in earlier stages of growth. The flowers of S. *chinensis* are much more sparsely arranged than those of S. *cernuus*, but in most other respects, the inflorescences of the two species are similar (Figs. 12, 13).

The inflorescence of *Houttuynia cordata* has been described in detail by Nozeran (1955). It is a spike with 4 conspicuous bracts at the base (some flowers, however, have small pedicels). Bracts higher up are much reduced to either scales or simple enations. The flowers show various degree of adnation of their pedicels with the bracts. However, in most cases this adnation is not superficially recognizable (Figs. 9, 15). In this species, Nozeran (1955) has reported a progressive transformation of complete flowers into staminate and pistillate ones within the same spike. Similar transformation has been observed by the present author.

Structures of both flower and inflorescence of *Anemopsis* have been described by Quibell (1941). The inflorescence is a highly condensed spike and is subtended by 6–8 petaloid bracts. The young inflorescence axis in early stages resembles a flower covered by bracts. The inflorescence axis is mainly made up of "sunken" pistils (Fig. 16). The bracts, which vary in number, are foliaceous and gradually decrease in size from base upwards (Fig. 5). Except for the lowermost bracts, the rest are adnate to naked flowers.

The inflorescence of *Gymnotheca chinensis* is also a spike, if one follows the terminology of Nozeran (1955). The bracts are not so conspicuous as those of *H. cordata* and *A. californica*. However, the gradual reduction in size of bracts from base upward is similar to the situation in *H. cordata*.

Flower

Flowers of *Saururus*, particularly S. *cernuus* show considerable variation in structure and number. An average flower of S. *cernuus* is pedicellate with 4 simple pistils and 6 stamens. Other combinations like 4–5, 4–7, 4–8, 5–7, 5–8, 3–4, and 3–6 have been observed. Serial sections of flowers of S. *cernuus* show the spiral arrangements of carpels and stamens. Carpels are very closely approximated to one another giving an impression of syncarpy. The stamens are hypogynous and are opposite the carpels (Fig. 2). Pistils show extensive stigmatic crests on adaxial sides of styles (Figs. 2, 4). The stamens are much longer than the styles. In S. *chinensis* flowers show the same variation as S. *cernuus*, but the pistils have shorter styles. Stamens in S. *chinensis* are perigynous and do not exceed the pistils in height.

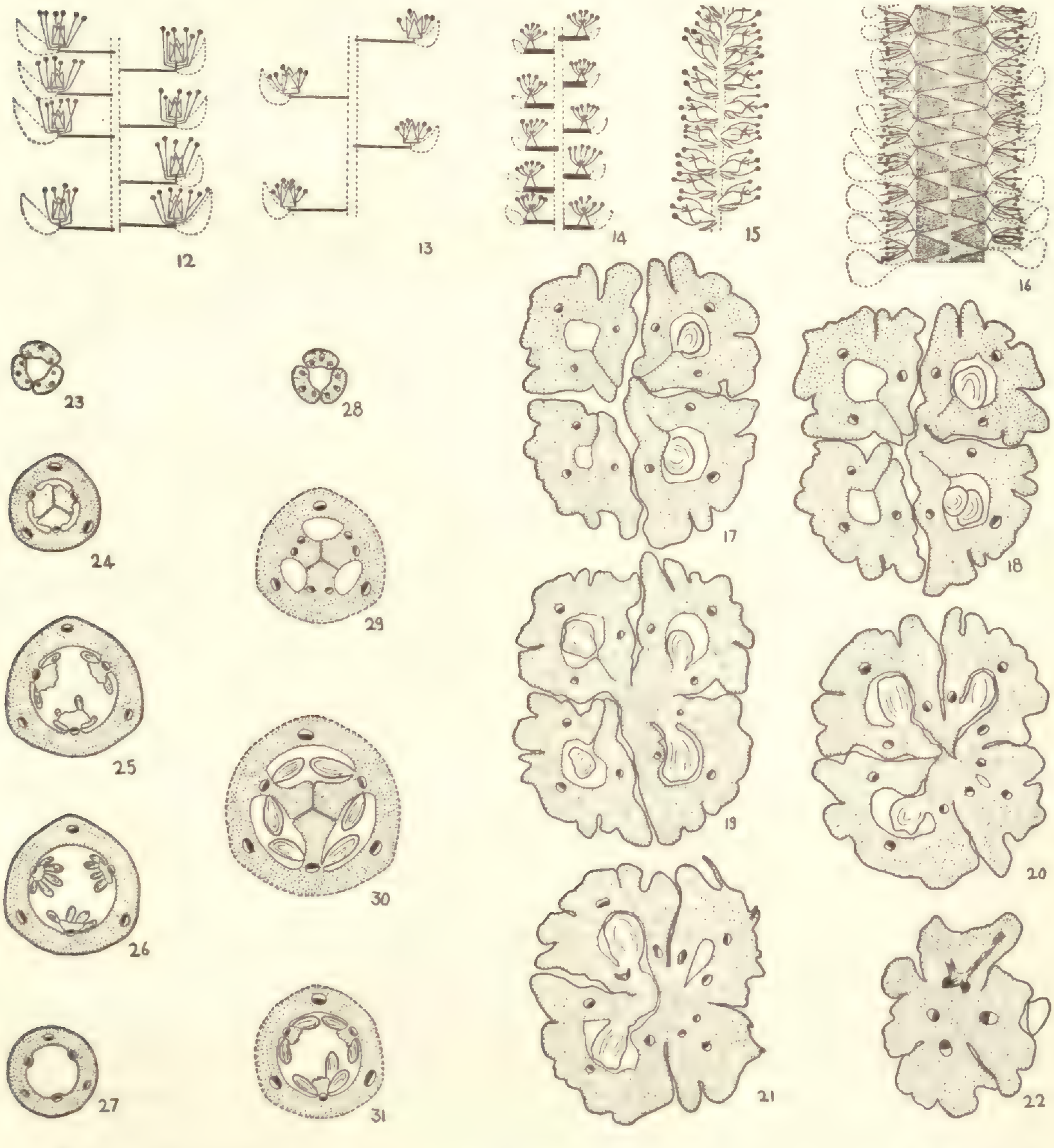
In *Houttuynia cordata*, the flowers are naked and have small pedicels. These

pedicels toward the inflorescence apex are further shortened or the flowers are sessile. The compound pistil is made up of three carpels, and the styles are free with wide stigmatic crests on their adaxial sides (Figs. 9, 10). In the arrangement of flowers, *Gymnotheca* resembles *Houttuynia.* According to the diagram of Decaisne (1845), the flower of *Gymnotheca chinensis* has a 4-partite pistil and 6 epigynous stamens (Fig. 14).

The inflorescence of *Anemopsis californica* has pistils buried in the "inflorescence axis". In these naked flowers, the compound pistil is made up of usually 3 carpels with free styles. The epigynous stamens are usually six in number. However, this number is subject to variation. The petaloid bract appears to be situated

Text Fig. 1. Figs. 1–4. *Saururus cernuus.* Fig. 1. A portion of branch showing the spiral arrangement of leaves and terminal inflorescences. Fig. 2. A flower with bract, stamens and pistils (note the warty structures on ovary). Fig. 3. Sectional view of pistil to show the position of ovules and vascular traces. Fig 4. Longisection of a carpel. Figs. 5–7. *Anemopsis californica.* Fig. 5. A small plant with roots, rhizome, rosette of leaves and an inflorescence. Fig. 6. Longisection of ovary showing placentation, flared margins of stigmatic crest and epigynous stamens. Fig. 7 Transection of same showing parietal placentation and incomplete septa. Figs. 8-11. *Houttuynia cordata.* Fig. 8. A portion of branch with leaves, stipules and inflorescence. Fig 9. A flower with a compound pistil and epicarpellary stamens. Short pedicel of flower is adnate to scale-like bract. Fig. 10. Longisection of pistil showing placentation and stigmatic crest. Fig. 11. Transection of ovary showing parietal placentation.

at the neck of the compound pistil. Developmentally it is adnate to the pistil along its length (Fig. 49). It is also interesting to note that in certain inflorescences bracts show a gradual change from base upwards from a petaloid bract to a petaloid stamen. This also followed by a highly reticulate venation pattern in the lowest bract to a highly reduced "dichotomous pattern" in bracts at the tip of inflorescence.



Text Fig. 2. Figs. 12–16. Diagrammatic sketches of portions of inflorescences of *Saururus cernuus*, *S. chinensis*, *Gymnotheca involucrata*, *Houttuynia cordata*, and *Anemopsis californica* respectively. Figs. 17–22. *Saururus cernuus*—Transverse sections of flower (stamens not included) at different levels to show spiral arrangement of carpels and also placentation, × 80. Figs. 23–27. *Houttuynia cordata*—Transection of compound pistil at different levels (diagrammatic). Figs 28–31. *Anemopsis californica*—Transection of flower (stamens not included) at different levels (diagrammatic).

Anatomy of the Flower

Saururus.—Anatomy of the flower has been recently described for S. *cernuus* by Murthy (1959). Carpellary traces* in the flower originate spirally. Serial sections also indicate the spiral arrangement of carpels. Although ventral margins of carpels are closely approximated or partially fused at the lowermost regions of 'pistil', the ventral traces remain free throughout their course. In certain cases the ventral and dorsal traces of each carpel merge at the apex and appear as though fused to form a common trace. It is also not uncommon to find ventral traces ending near the base of styles. Ventral traces give off branches to the two ovules present in each carpel; placentation in the carpel has been here interpreted as laminar (Figs. 3, 4, 17–22).

The anatomy of the flower of *Saururus chinensis* is similar to that of S. *cernuus* with, however, a few deviations. Stamen traces arise as branches from the dorsal traces of carpels. The ventral trace invariably merges in the stigmatic region with the dorsal trace to form a thick common trace. Unlike S. *cernuus*, there is no conspicuous style in S. *chinensis*.

Houttuynia.—The naked flowers are trimerous and bracteate (Fig. 9). The vascular bundle from the inflorescence axis extends into the cortex and becomes the trace for the flower. It branches to form two traces, one leading into the bract and the other into the flower proper (Figs. 32, 33). The bract trace may or may not ramify depending on whether the bract is "leaf-like" or scaly. The remaining trace branches at different levels to form three independent carpellary traces which show a spiral arrangement (Fig. 32). Each carpellary trace gives rise to a dorsal and two ventral traces (Figs. 32, 34–39). The ventral traces of adjacent carpels fuse together to form "compound ventral trace" or placental trace. Each placental trace gives off branches which supply the ovules. The placental trace when it reaches the style bases separates and extends into the respective styles. Ventral traces together with the dorsal trace go into the style and all three remain separate. No instance of their fusion at the tip of style was found. Placentation is parietal and ovules are present only in placental region where the ventral traces have fused to form the placental trace. Stamen traces are formed much later than the ventral traces and arise about the middle of the pistil from the carpellary dorsal trace (Figs. 32, 40–48).

Anemopsis.—Quibell (1941) has given in sufficient detail the vascular anatomy of the flower. As in other genera, a single trace from the inflorescence axis diverges and branches to form a bract trace and a "flower trace" (Figs. 49-52). Although the bract is adnate to the pistil, the bract-trace is free throughout (Figs. 49–66). Each "flower trace" branches to form ventral and dorsal traces. Each carpel receives two ventral traces and a dorsal trace. As in *Houttuynia*, ventral traces of adjacent carpels immediately fuse to form the placental trace whose branches supply the ovules. At about the base of style, the placental traces separate to give ventral traces which pass into the respective styles. Each ventral trace, on its way

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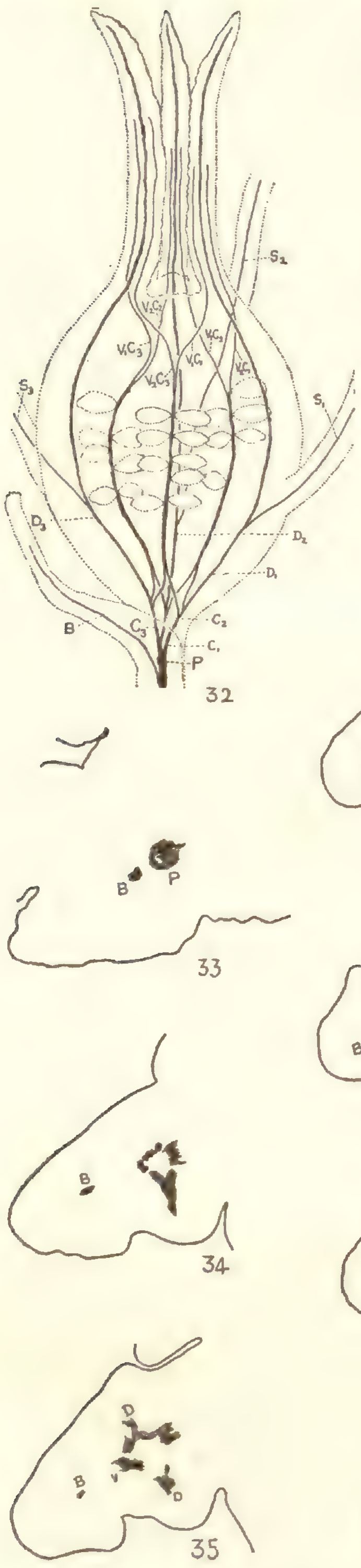
* For the sake of convenience the term 'trace' has been used in describing the vasculature of different organs of flowers.



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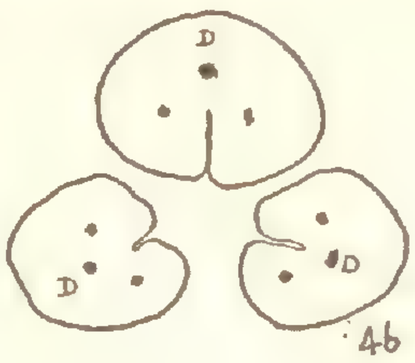

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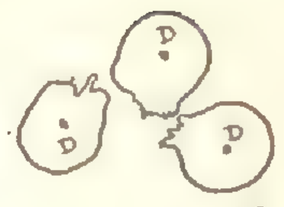

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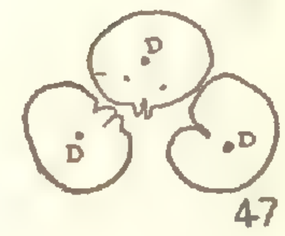

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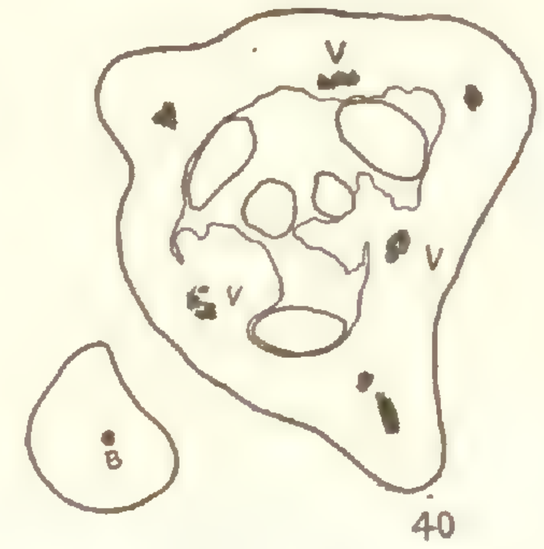

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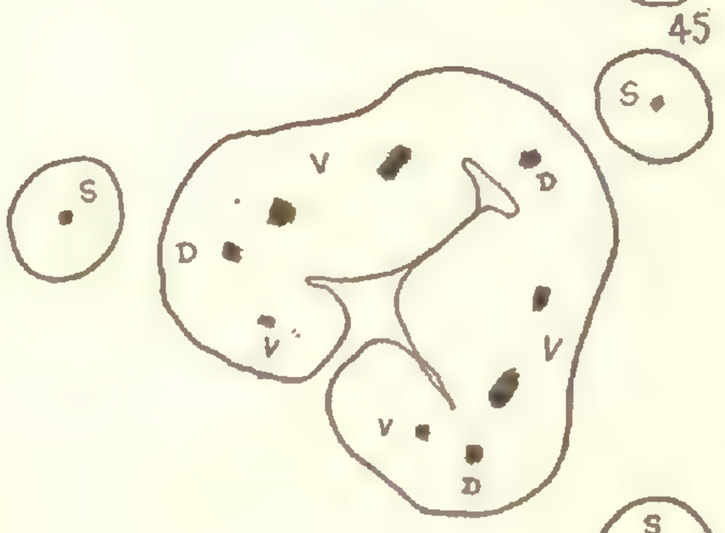

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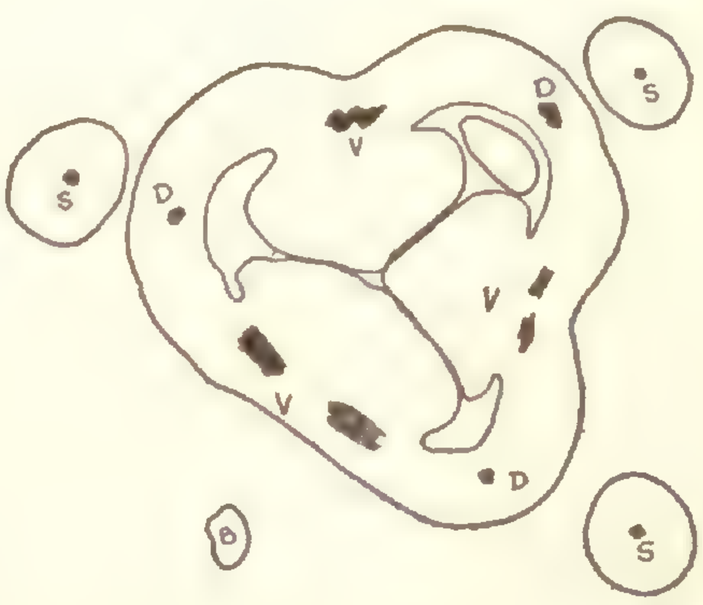

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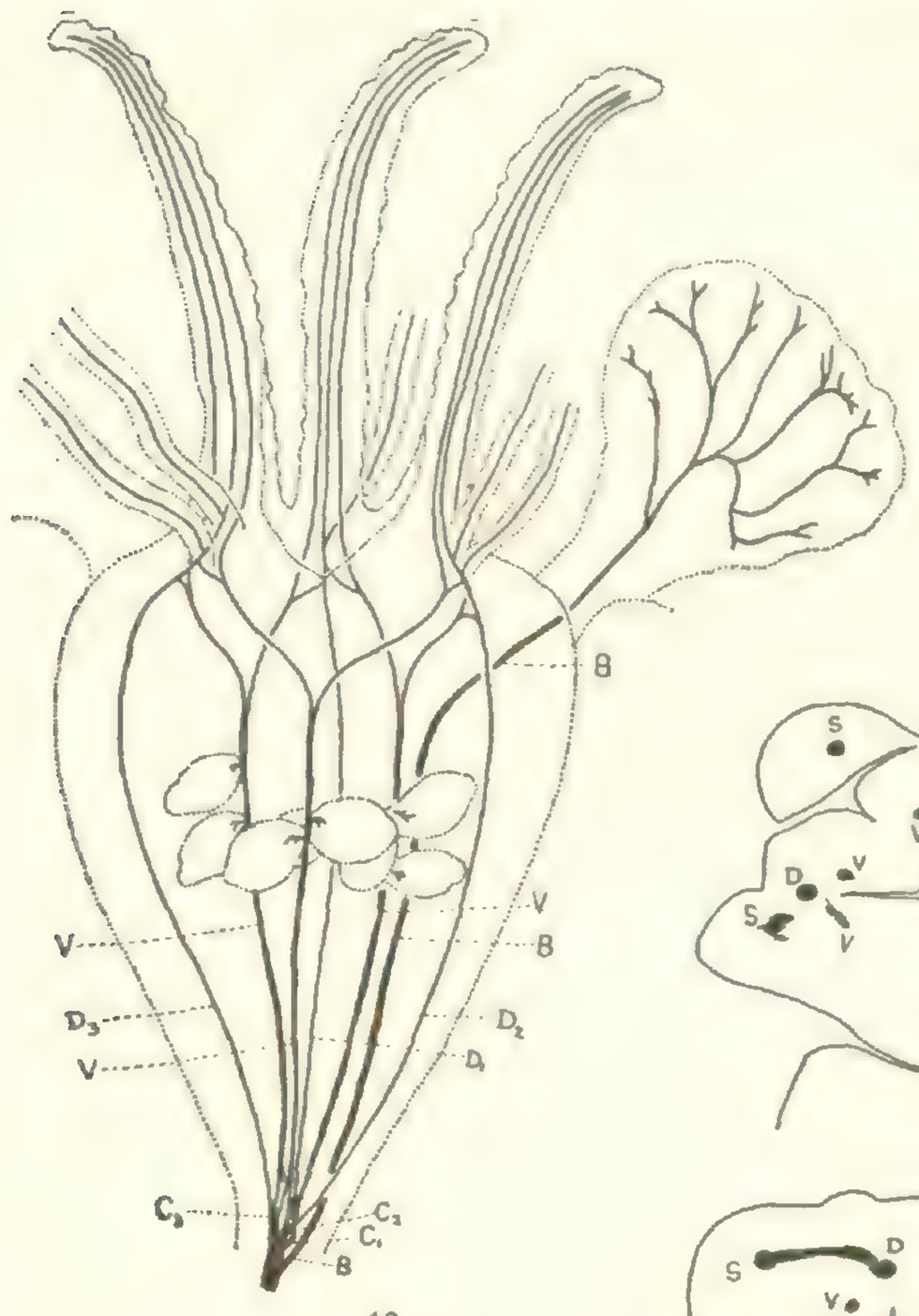
Text Fig. 3. *Houttuynia cordata*. Fig. 32. Diagrammatic sketch of a flower showing vascular traces. Figs. 33–48. Transections of flower at different levels to show vascular anatomy of the flower (B, bract trace; $C_{1, 2, 3}$, traces of three carpels; D, dorsal trace of carpel; $D_{1, 2, 3}$, dorsal trace or common trace of dorsal trace of carpel and stamen trace; P, pedicel trace; S, stamen; $S_{1, 2, 3}$, stamen traces; $V_1 C_1$, $V_2 C_1$, $V_1 C_2$, $V_2 C_2$, $V_1 C_3$, $V_2 C_3$, ventral traces of respective carpels; V, ventral trace), × 100.



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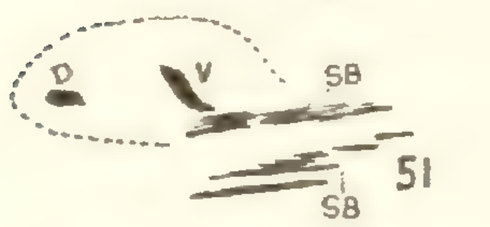

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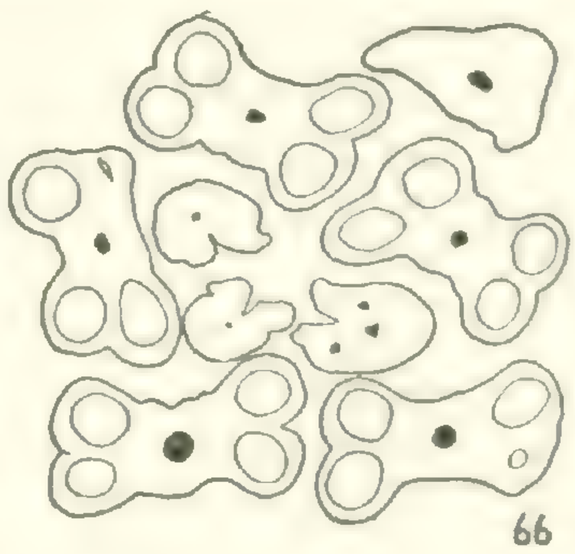

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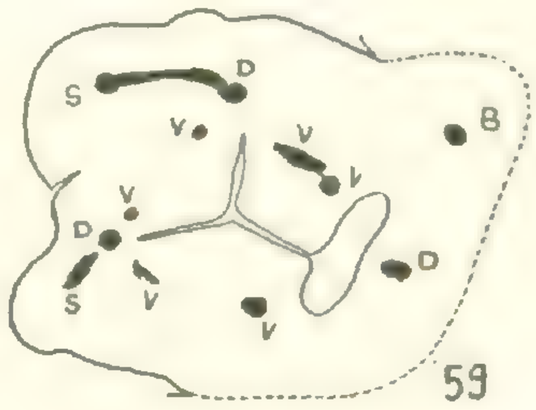

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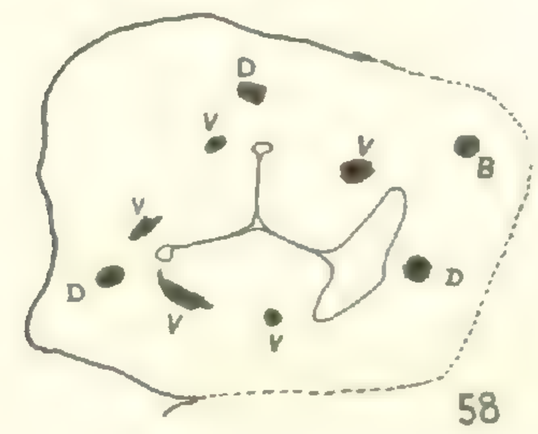

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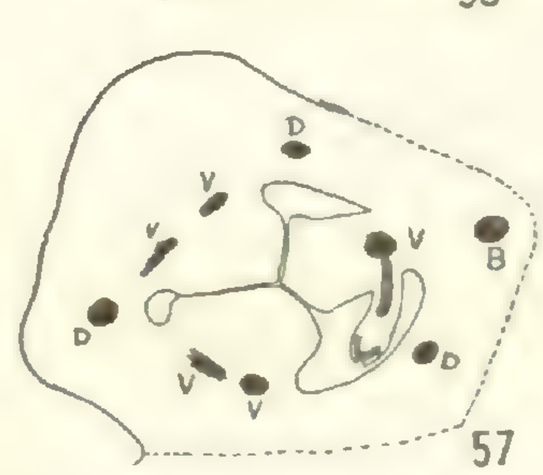

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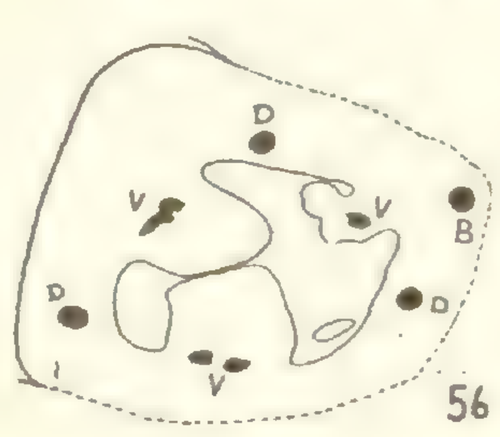

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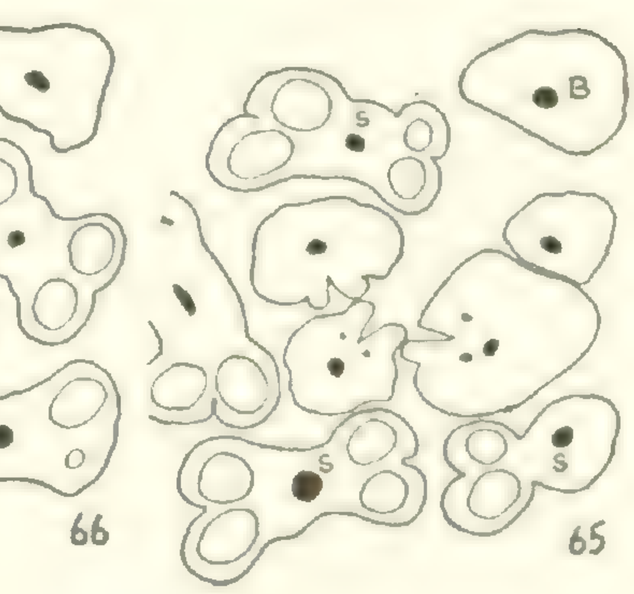

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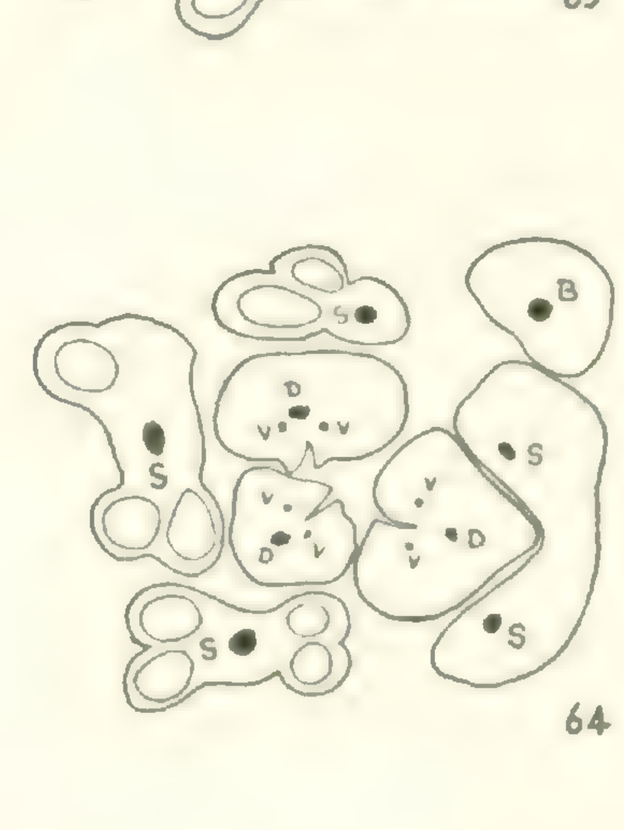

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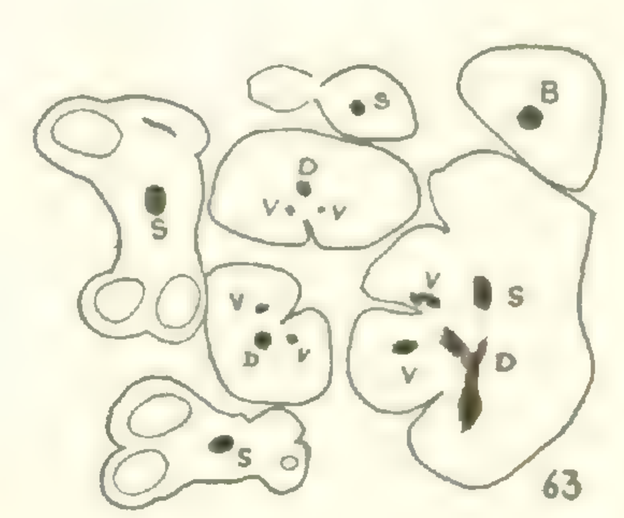

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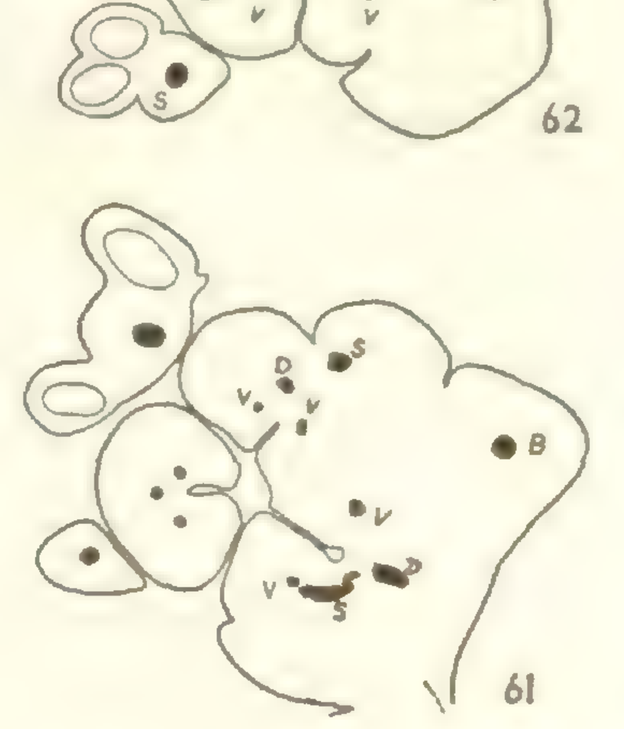

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Text Fig. 4. *Anemopsis californica*. Fig. 49. Diagrammatic sketch of a flower to show vascular traces. Figs. 50–66. Transections at different levels of a flower showing vascular traces (B, bract; $C_{1, 2, 3}$, carpel traces; D, D_1, D_2, D_3, dorsal traces; SB, axial bundle of inflorescence; S, stamen trace; V, ventral trace), × 100.

to the base of the style, is connected with the dorsal trace. The dorsal trace with the other two ventral traces extend into the style (Figs. 58–66). At the base of style the dorsal bundle gives off branches to one or two stamens. Placentation is parietal as in *Houttuynia*.

Carpels and Placentation

A considerable variation has been found in the structure of carpels and in the organization of pistils in the Saururaceae. Carpels in *Saururus cernuus* are free throughout except at the base, a little above the short pedicel where they show a lateral concrescence (Figs. 17–22). They arise in a spiral fashion, a fact clearly seen in serial sections. There is considerable elongation above the ovule-bearing region. In *Houttuynia*, *Gymnotheca* and *Anemopsis*, clearly recognizable stylar regions are found. Furthermore, in all these three genera, the pistil is "compound" (in the sense that the ovary is syncarpous and the styles are free) (Figs. 6, 7, 10, 11).

In *Saururus cernuus*, the folded laminae are conspicuous and the ventral traces are present away from the carpellary margins. During organization of the pistil, these laminar margins of adjacent carpels undergo concrescence which is to a considerable extent mistaken for axile placentation; placentation here is actually laminar. The lateral concrescence of adjacent carpels may be attributed to a case of "incipient syncarpous tendency" (Bailey and Swamy, 1951).

The compound pistil of *Houttuynia* and *Anemopsis* is formed as a result of lateral approximation and concrescence of carpellary margins of adjacent carpels. This concrescence is also accompanied by fusion of ventral traces of adjacent carpels. Only in this region of concrescence of carpellary margins and also of lateral or ventral traces is parietal placentation organized. The sterile margins of carpels also undergo concrescence to form septa; as a result the compound pistil appears to be three-loculed (Figs. 23–31). This kind of incomplete septation is found in the upper part of the pistil of *Houttuynia cordata;* it extends almost half the depth of the pistil in *Anemopsis*.

Embryology

Saururus cernuus.—Microsporogenesis and male gametophyte.—The wall of a young anther consists of four layers, an epidermis, hypodermal layer, middle layer and an innermost tapetal layer. The mature anther wall has an epidermis with cutinized outer wall, hypodermal layer with characteristic fibrous thickening and

Text Fig. 5. *Saururus cernuus*. Fig. 67. A portion of anther wall showing epidermis, hypodermal layer with endothecial thickening, crushed middle layer, and a tepetal layer, × 333. Figs. 68–71. Stages in the formation of microspore, × 833. Fig. 72. A young ovule showing megaspore mother cell and primary parietal cell, × 333. Fig. 73. Nucellus showing division of nucleus of megaspore mother cell, × 666. Fig. 74. Same at a later stage with a dyad, × 666. Fig. 75. Shows division of lower dyad cell, × 666. Fig. 76. A linear row of three cells or a "triad", the lowermost being the megaspore, × 666. Fig. 77. Degeneration of middle cell of a linear "triad". Note vacuolation in the lowermost cell, × 666. Fig. 78. The upper two cells of a "triad" have degenerated and the lowermost has become the functional megaspore, × 666. Fig. 79. Mature embryo sac with the egg apparatus and secondary nucleus, × 666. Fig. 80. Longisection of a young seed showing embryo, cellular endosperm and a lower caecum containing a hypertrophied nucleus, × 147. Fig. 81. An enlarged view of a hypertrophied nucleus in a caecum, × 666. Fig. 82. Longisection of seed showing cellular endosperm, embryo and perisperm (Emb, embryo; En, endosperm; Nu, nucellus or perisperm), × 35.

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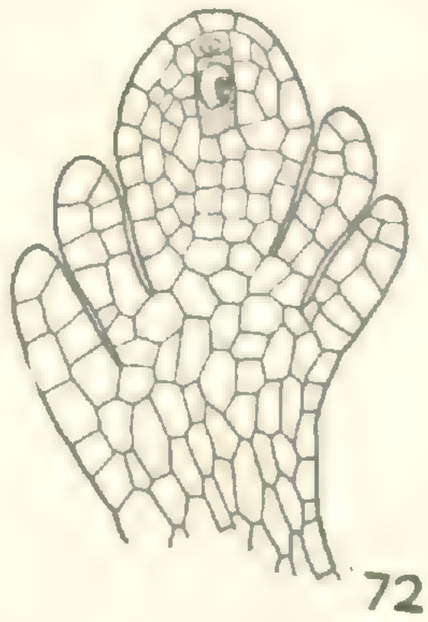
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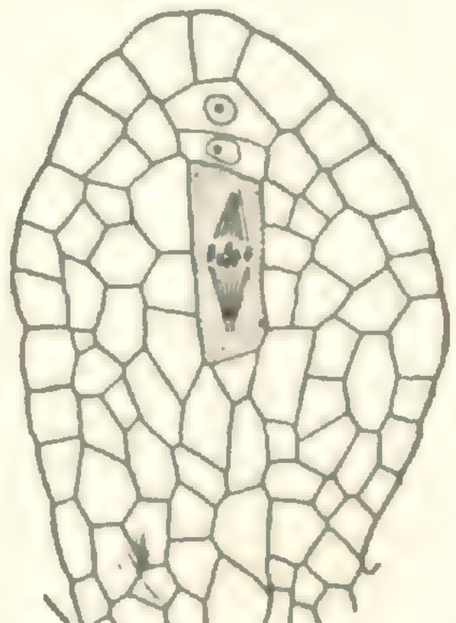
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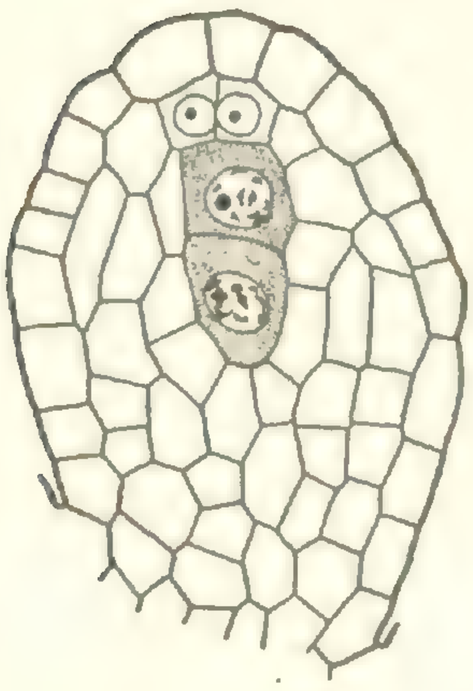
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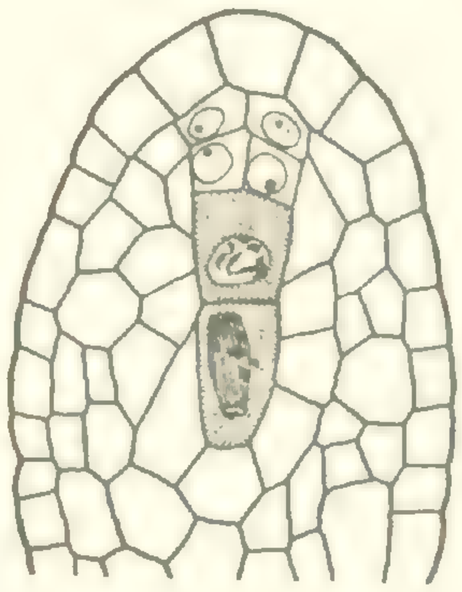
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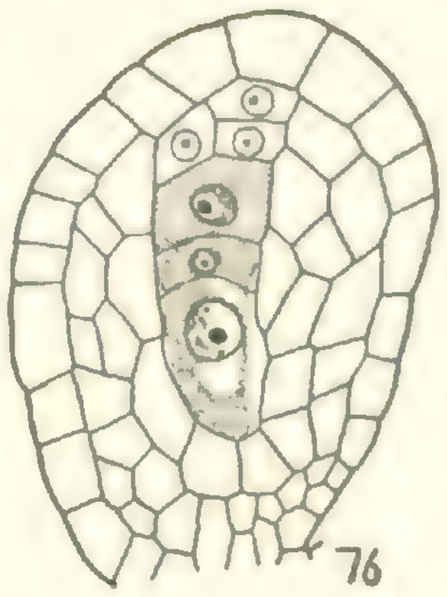
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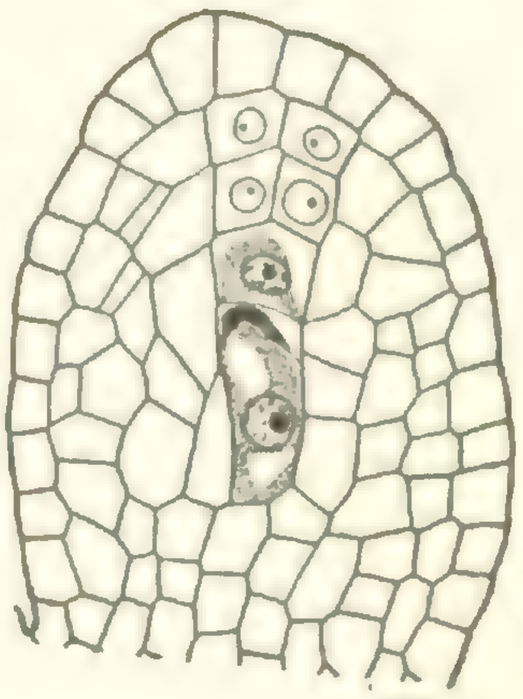
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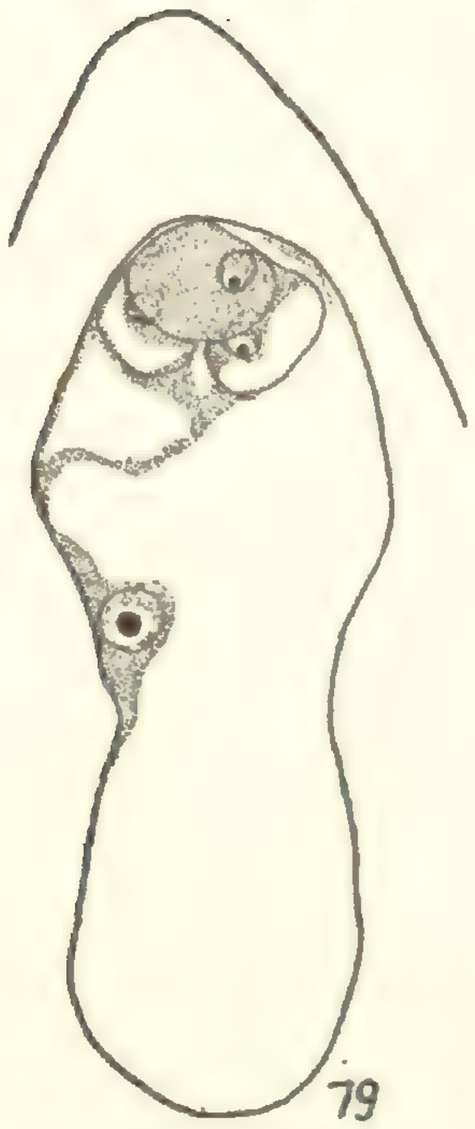
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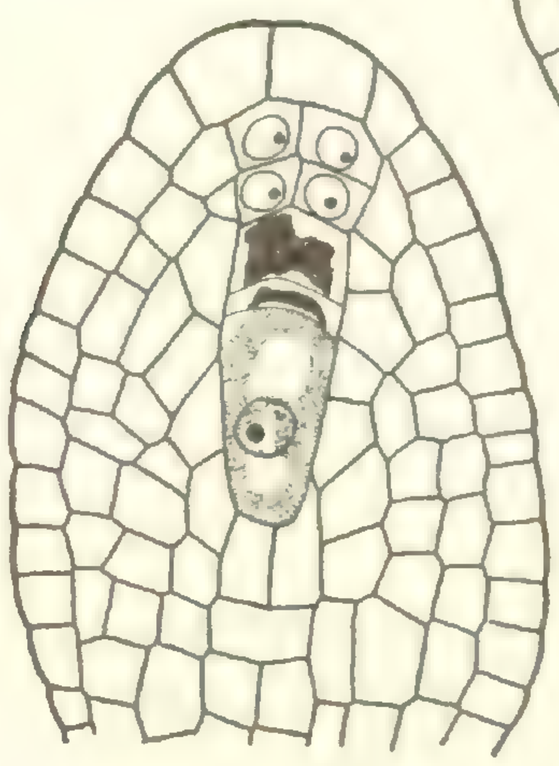
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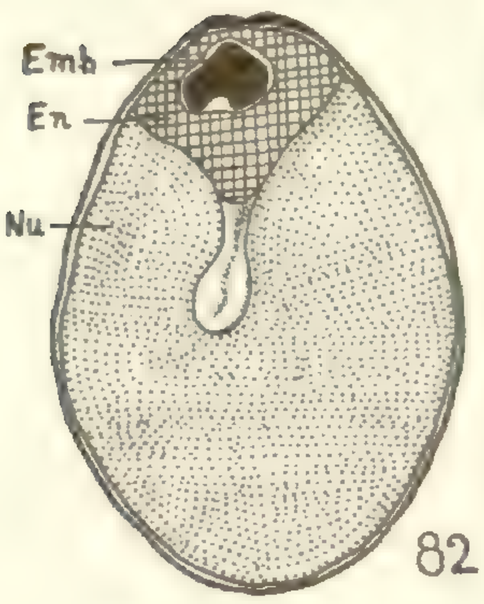

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tapetal layer with binucleate cells (Fig. 67). The sporogenous cells differentiate themselves into microspore mother cells which undergo meiosis and form first microspore tetrads and then microspores (Figs. 68–71).

Megasporogenesis and female gametophyte.—The crassinucellate ovules are orthotropous-bitegmic and borne on laminar placentae (Figs. 3, 4, 19–21). The micropyle is organized by both the integuments. The outer integument is two layered; the inner is three layered. A single hypodermal archesporial cell is differentiated in a young ovular primordium. It undergoes a transverse division to form primary sporogenous and parietal cells (Fig. 72). The primary parietal cell, by anticlinal and transverse divisions, forms a parietal tissue of about 8 superposed cells (Figs. 73–78).

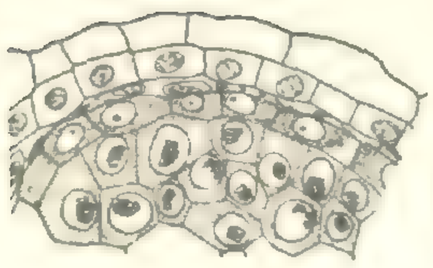
The primary sporogenous cell divides meiotically to form a dyad (Fig. 74). During further development, the lower dyad cell divides and the upper does not (Figs. 75–76). Thus, the dyad gives rise to a "triad" or a linear row of three cells (Figs. 76, 77). Of these three cells, the upper two degenerate and the lowermost develops into the embryo-sac (Figs. 77–79). The antipodal cells are ephemeral and seldom seen in a mature embryo sac. The egg apparatus is situated at the micropylar end and no case of fertilization was observed.

Endosperm.—The endosperm nucleus divides transversely to form a micropylar chamber and a chalazal chamber. The chalazal chamber behaves as a haustorium and the nucleus becomes hypertrophied. The mature seed encloses massive perisperm and a little endosperm surrounding the developing embryo (Figs. 80–82).

Houttuynia cordata.—Microsporogenesis and male gametophyte.—Microsporogenesis and male gametophyte development follow the sequence given for *Saururus cernuus*, but with some differences. Division of the microspore mother cell shows various cytological abnormalities resulting in the formation of sterile pollen. Frequently, micronuclei are seen in microspore tetrads. Very rarely free microspores are observed (Figs. 83–88).

Megasporogenesis and female gametophyte.—The bitegmic orthotropous ovules are borne on parietal placentae (Figs. 25, 26, 89–90, 99). The ovular primordium shows a hypodermal archesporium (Figs. 89, 90). Similar to *S. cernuus*, the outer integument is made up of two layers and inner of three layers (Fig. 99). Again, the micropyle is organized by both the integuments (Fig. 99). An archesporial cell of hypodermal origin functions directly as the megaspore mother cell (Figs.

Text Fig. 6. ***Houttuynia cordata.*** **Fig. 83. A portion of anther showing anther wall and** sporogenous tissue; anther wall shows epidermis, hypodermal layer, crushed middle layer and tapetal **layer, × 333. Fig. 84. Same at a later stage; note binucleate tapetal cells, × 333. Fig. 85. Mature** anther wall showing endothecial thickenings in hypodermal layer; note also microspores, × 333. Fig. 86. Metaphase I in microspore mother cell, × 666. Fig. 87. Same showing anaphase I; note the irregularity in the movement of chromosomes, × 666. Fig. 88. Microspore tetrad with a few micronuclei, × 666. Fig. 89. Ovular primordium with integumental and archesporial initials, × 333. Fig. 90. A later stage of the same, × 333. Fig. 91. First division of archesporial cell, × 666. Fig. 92. A portion of nucellus showing a dyad, × 666. Fig. 93. Same showing the lower cell has divided to form a linear row of three cells, × 666. Fig. 94. Uninucleate embryo sac with degenerated upper dyad cell and megaspore, × 666. Fig. 95. A binucleate embryo sac, × 666. **Fig. 96. An embryo sac showing hooked** synergids, egg, two polar nucleii and degenerated antipodal cells, × 666. Fig. 97. A mature embryo sac with egg apparatus, secondary nucleus and antipodal cells, × 333. Fig. 98. A stage showing probably zygote; first division of endosperm nucleus has resulted in two cells, the lower one being a haustorium, × 333. Fig. 99. A young ovule showing the developing megaspore, massive nucellus, and two integuments, inner three-layered and outer two-layered, × 133.



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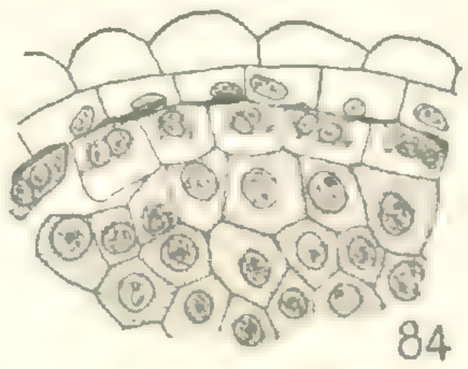

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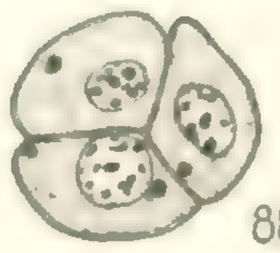

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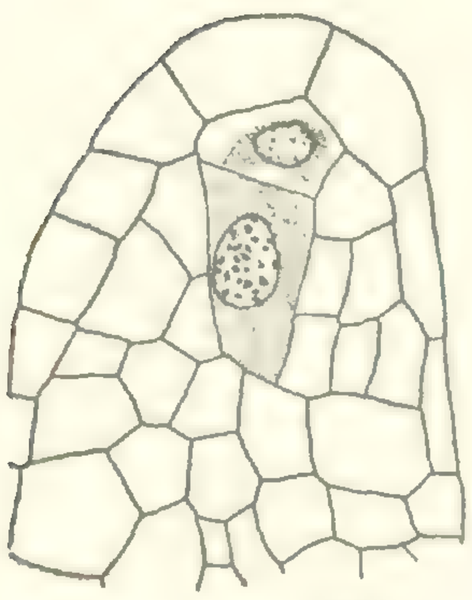

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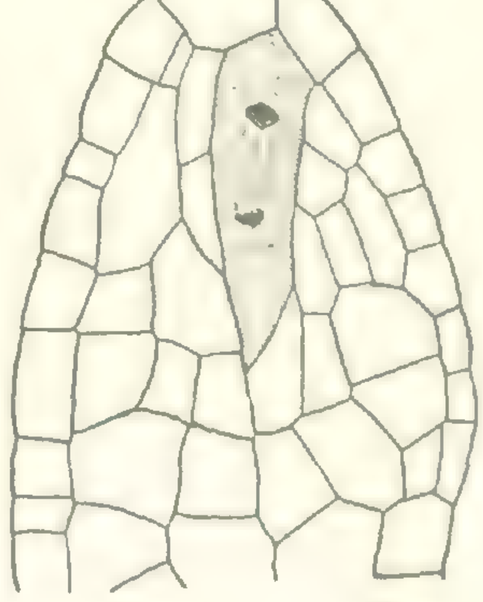

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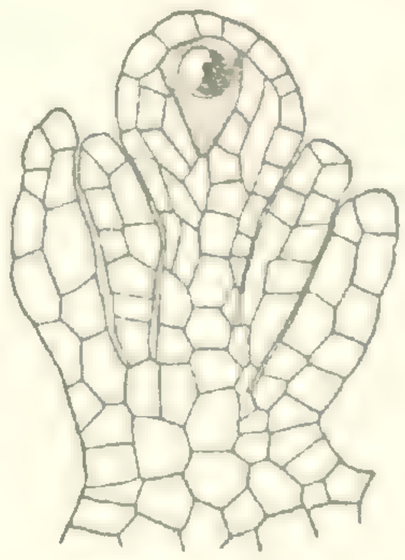

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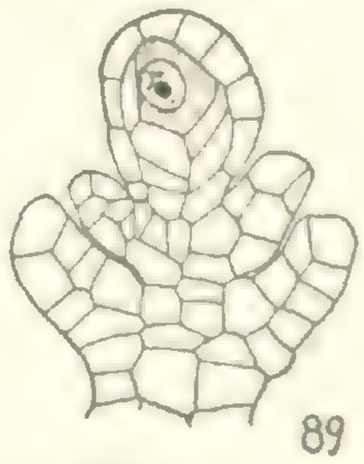

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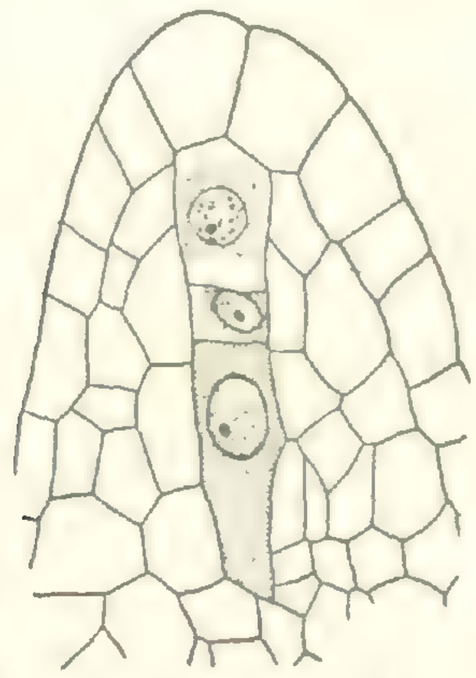

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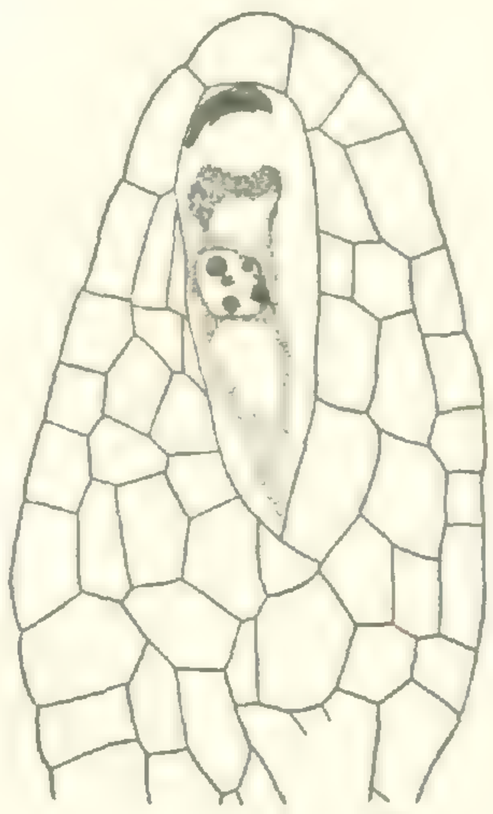

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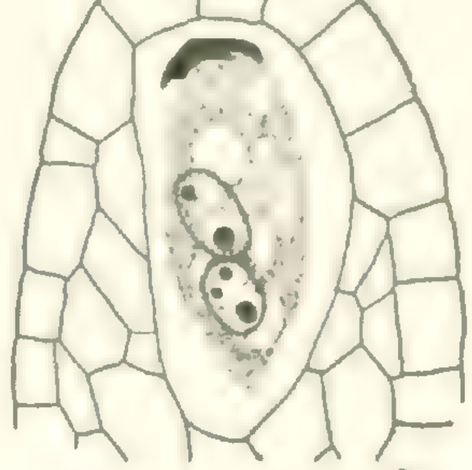

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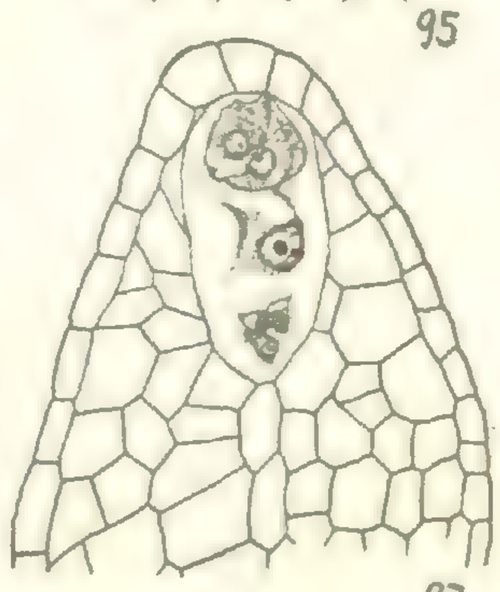

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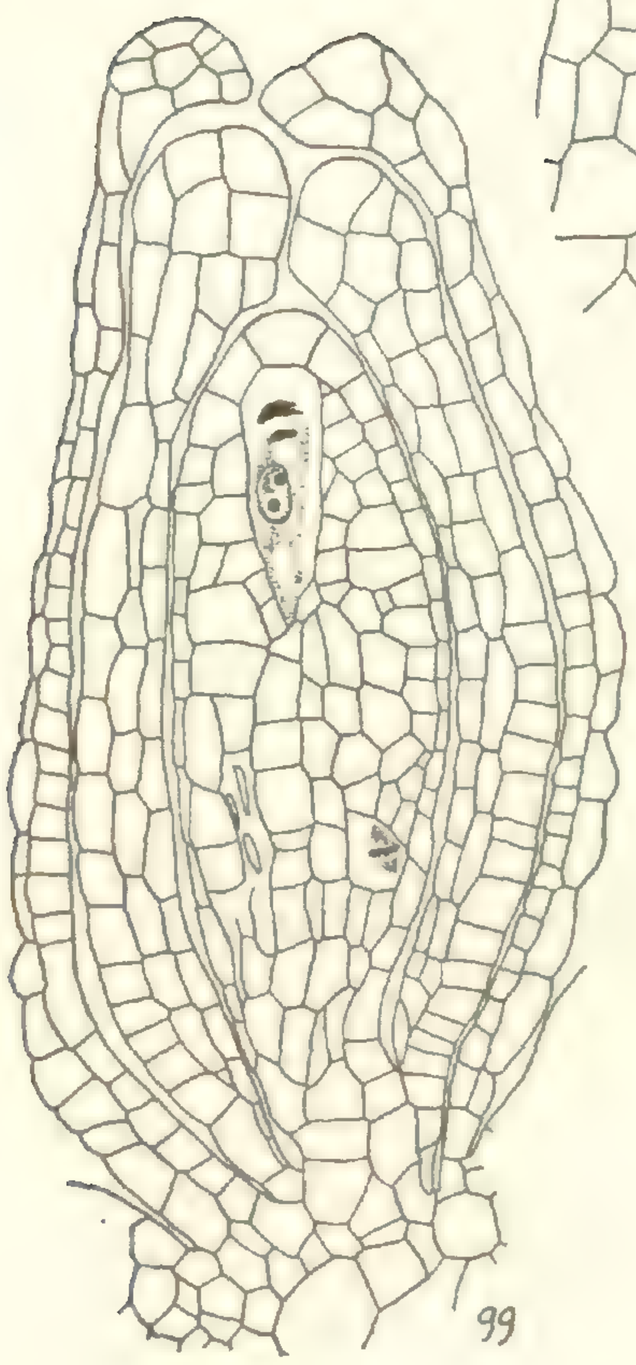

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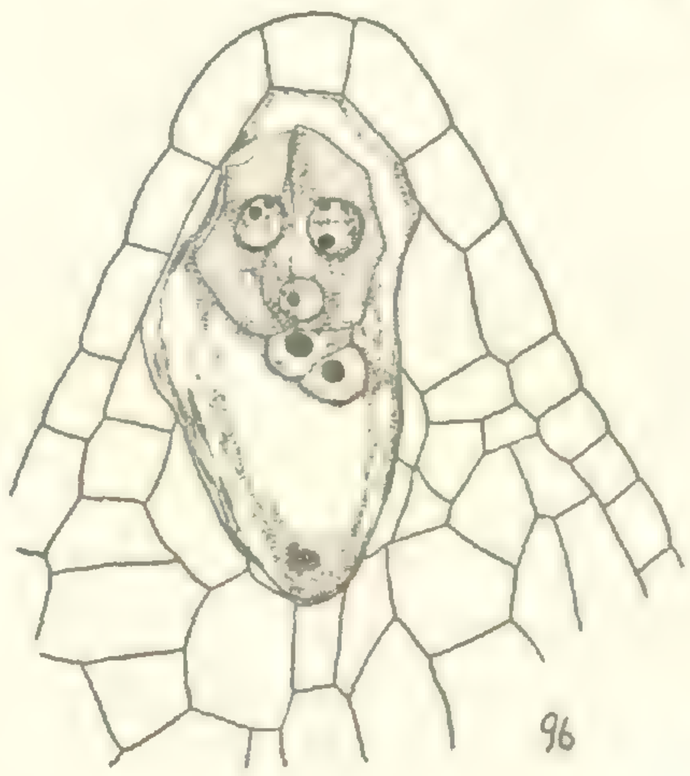

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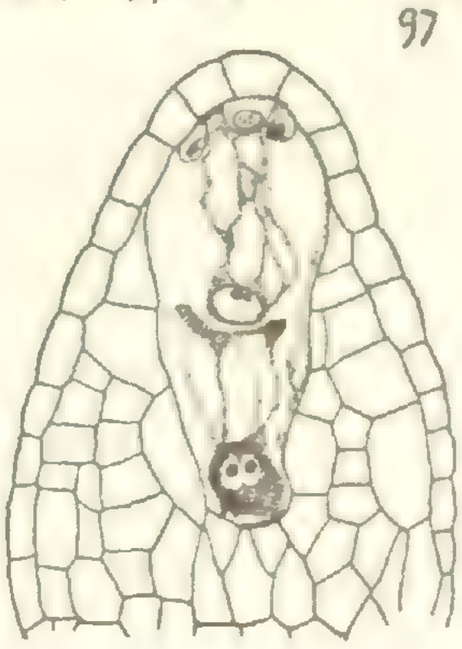

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91–98). The megaspore mother cell divides meiotically to give a linear row of three cells of which the lowermost is the megaspore that develops into the embryo sac (Figs. 91–98). Antipodal cells in the mature embryo sac are epheremal but in some cases these cells are seen in mature embryo sacs (Figs. 96–97). The egg apparatus in the micropylar end is made up of an egg cell and two hooked synergid cells (Fig. 96). Here, also, fertilization stages were not observed.

Endosperm.—The endosperm behaves as in *S. cernuus* (Fig. 98). In mature seeds often only endosperm and perisperm were observed. The embryo was not seen.

Anemopsis californica.—Microsporogenesis and male gametophyte.—Microsporogenesis and development of male gametophyte simulate those of *Saururus cernuus* and *Houttuynia cordata* (Figs. 100–105).

Megasporogenesis and female gametophyte.—The orthotropous bitegmic ovules are found on parietal placentae as in *H. cordata* (Figs. 6–7, 30–31). A hypodermal archesporial cell is differentiated and divides to form a parietal cell and primary sporogenous cell (Fig. 106). The primary sporogenous cell divides meiotically to give a row of three cells as in other genera (Fig. 107). The lowermost cell functions as the megaspore and develops into an embryo sac (Figs. 107–110). Stages in fertilization have not been observed.

Endosperm.—The earlier stages of endosperm development are like those of *Houttuynia* and *Saururus cernuus*. In the mature seed, massive perisperm, degenerated embryo and endosperm were observed.

Fruit

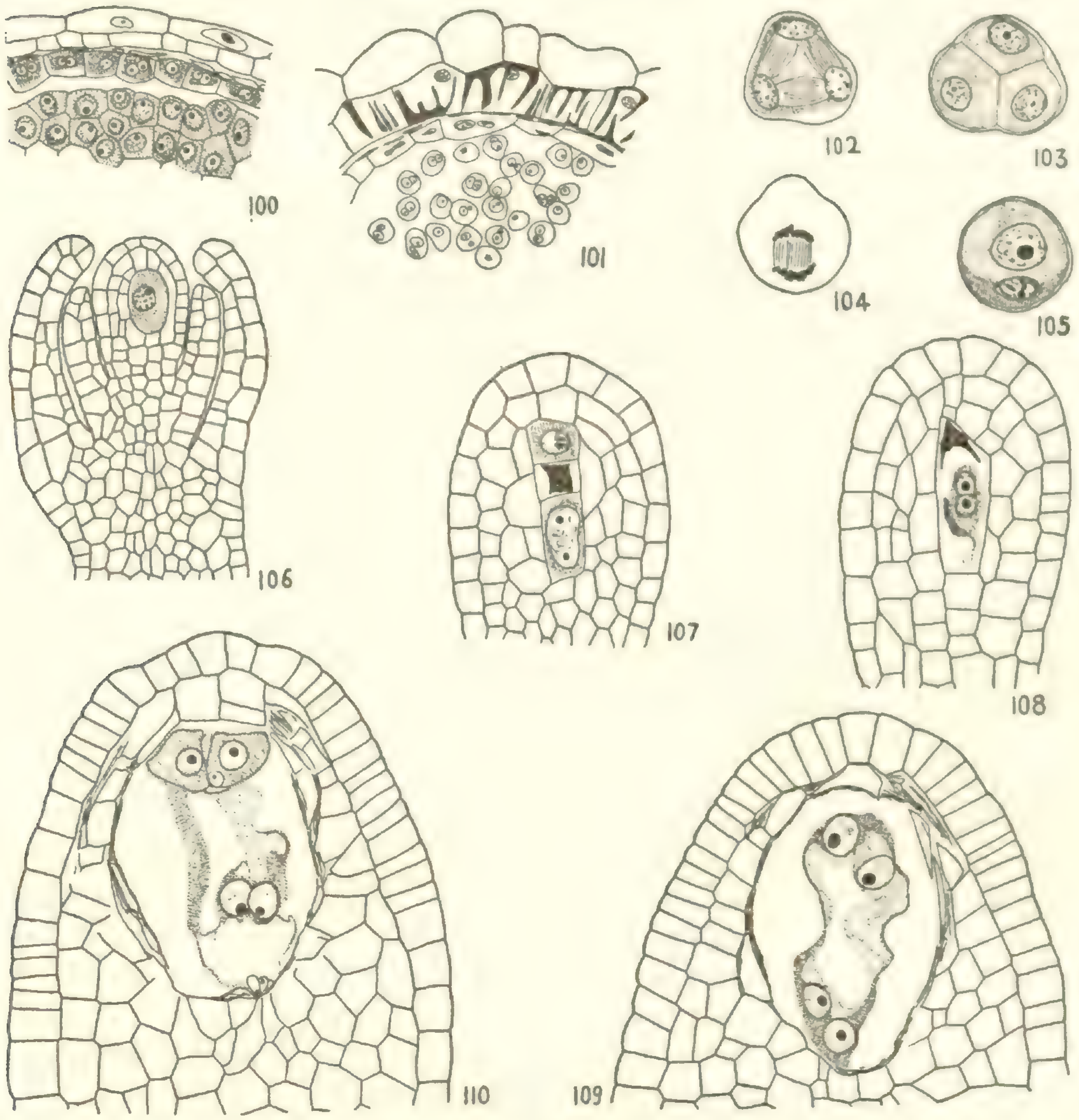
In *Saururus* simple pistils organize the fruit. The pericarp becomes dry-fleshy enclosing a single seed. No case of fruit dehiscence has been observed. Furthermore, there is no stony endocarp developed in the pericarp. On the other hand, seed coat becomes very hard and often closely abutting the inner wall of pericarp. The fruit is here interpreted as a berry.

In *Houttaynia* and *Anemopsis* the fruits are dehiscent capsules with many smaller seeds. The dehiscence of fruit occurs at the apical region by the disintegration of fused ventral margins in the middle region of three free styles. In a dehisced fruit a circular port is seen at the top of the ovary leaving the styles free.

Discussion

Observations on inflorescence of the six species of Saururaceae show an interesting evolutionary trend, probably guided by two processes: 1. reduction, and 2. cohesion and adnation. Of the four genera, *Saururus* shows the least change by the above processes.

The "common stalk" of flower and bract shows various degree of reduction. In *Saururus* the "common stalk" is much elongated and shows stages of its reduction. Further reduction of the same has resulted in a condition seen in *Houttuynia* in possessing a recognizable "common stalk" (Figs. 12, 13, 15). *Anemopsis*, on the other hand, shows the final culmination where the pistils appear embedded in the "inflorescence axis" and the bract appears to be situated at the top of the ovary (Figs. 16, 49). In all genera this process of reduction is associated with



Text Fig. 7. *Anemopsis californica.* Fig. 100. A portion of anther wall showing epidermis, hypodermal layer, crushed middle and tapetal layers surrounding the sporogenous tissue, × 333. Fig. 101. same at a later stage showing endothecial thickenings in the hypodermis; two-celled microspores are seen, × 333. Figs. 102–105. Stages in the formation of microspores, × 666. Fig. 106. A young ovule showing megaspore mother cell and two integuments; note parietal cells, × 333. Fig. 107. A portion of nucellus showing a linear row of 3 cells of which the lowermost develops into an embryo sac, × 666. Fig 108. Same at a later stage showing a 2-nucleate embryo sac with upper two degenerated cells, × 666. Fig. 109. A portion of nucellus with a 4-nucleate embryo sac, × 666. Fig. 110. Mature embryo sac with egg apparatus, two polars and 3 degenerating antipodals, × 666.

concomitant cohesion and adnation of floral parts. By a process of reduction in the number and cohesion of carpels, the polycarpellate condition seen in *Saururus* has resulted in the three or four carpelled syncarpous condition found in the other genera. This change has been accompanied by the adnation of stamens to carpels and is exhibited by *Houttuynia*, *Gymnotheca* and *Anemopsis*. The genus *Anemopsis* has an inferior ovary, a feature that has resulted by their "sinking into" the inflorescence axis.

The phenomena mentioned above may also be explained in the light of floral anatomy. Although the bract appears to be a simple structure, it is very difficult to see where the bract begins and where it ends. It is morphologically intriguing to consider the trace of the "common stalk" as a "compound" one of bract and flower pedicel. This condition has been interpreted in *Saururus cernuus* as a case of adnation of flower to bract, by Murthy (1959).

Present observations show that only the pedicel of the flower is adnate to the bract; this feature is evidenced by vascular anatomy of *Houttuynia* and *Gymnotheca*. In *Saururus, Houttuynia* and *Gymnotheca,* the bract tends to remain free from the flower proper. But, in the case of *Anemopsis,* however, the bract is adnate to the pistil. This feature is of secondary derivation for the bract trace is completely free from the flower. This secondary condition is, probably, due to "development sinking-in" of the pistil. It can also be interpreted as a case of lateral concrescence of compound pistils in the inflorescence.

In *Saururus cernuus,* stamen traces are formed before the carpellary traces are differentiated. But in S. *chinensis,* vascular anatomy indicates that stamens have originated subsequently from the dorsal carpellary trace. This specialization has proceeded in increasing degree in *Houttuynia, Gymnotheca* and *Anemopsis* where the stamens are perigynous or epigynous.

In *Saururus* ventral traces are as prominent as the dorsal traces; they remain free from one another throughout their course except at the stylar tip where they show signs of fusion. Similar behavior of ventral and dorsal traces is seen in *Houttuynia* and *Anemopsis;* their fusion in the stylar tip is seldom observed. Besides, in these two latter genera, ventral traces of adjacent carpels fuse to form a placental trace. *Anemopsis* shows a unique feature in that the ventral trace has independent connections with the dorsal trace (Fig. 49). The exact significance of these connections is not known.

To begin with, the flower gets a single trace from the inflorescence axis in *Saururus, Houttuynia* and *Anemopsis.* Such a feature has been reported in many angiosperms. Puri (1951) in his review paper suggested that highly reduced flowers received just one trace. Whether this condition is simple by primitiveness or by reduction remains to be critically examined. As far as the present observations go, it seems that traces of different organs have undergone fusion to form a single composite trace.

The Saururaceae show both hypogenous and epigynous conditions. The problem then arises as to how the epigynous condition has been achieved. The problem of origin of the inferior ovary has been highly debated for a long time. Douglas (1944) in her comprehensive review has discussed different views regarding morphology of the inferior ovary. Of the many views postulated, only two have remained prominent; they are appendicular and axial views.

It is beyond doubt that in all genera of Saururaceae except *Saururus cernuus* stamens have fused with the carpels. In *Houttuynia* and S. *chinensis* stamens are situated half way up on the pistil. *Anemopsis* and *Gymnotheca* have their stamens on the ovary just below the styles. These clearly show that concrescence of certain

floral parts (here stamens) with the pistils has given rise to epigyny. This is in support of the views expressed by van Tieghem (see Puri, 1951, 1952; Eames, 1931).

In *Anemopsis*, besides the fusion of stamens with the ovary, there is developmentally a concrescence of pistils resulting in a massive spike. This condition has given an impression that pistils have "sunken". Adnation of the bract, with its free trace, to the pistil is an additional evidence to show that the ovary wall is made up of tissues other than that of the ovary wall itself.

Prior to syncarpy and epigyny, profound morphological and anatomical changes have taken place in flowers of the Saururaceae. These changes have been well preserved in the genus *Saururus*. The carpels with their respective stamens are arranged "spirally". The last-formed carpel does not possess a stamen or stamens. This detail suggests that the flowers of *S. cernuus*, adnate to bracts, are not actually simple; they are, probably, derived from a structure similar to an "inflorescence". Absence of an axial tissue, development of a terminal normal or abortive carpel with or without a stamen or stamens, and close telescoping of simple pistils suggest that the flower is of the "sympodial type". Each flower then represented by a carpel with its own stamen or stamens. A similar analogy can be traced in the flowers of Chloranthaceae (Cardemoy, 1863; Hooker, 1890). However, this idea has been contradicted on the basis of the absence of supernumerary structures in the flowers of Chloranthaceae (Swamy, 1953).

The successive arrangements of simple pistils with their associated stamen or stamens lead to two problems—nature of epigyny or perigyny in a simple pistil and same in compound pistil. In the case of *Saururus chinensis* the stamen or stamens are perigynous. This can be interpreted as a case of adnation. Syncarpous gynoecium also shows perigynous and epigynous conditions. It is difficult to say whether the cohesion of carpels appeared first or adnation of stamens to carpels. Available evidences, however, show in the Saururaceae that adnation of stamens to carpels appeared first as exemplified by *S. chinensis*. So, the flowers of *Hauttuynia* and *Anemopsis* suggest that they are made up of three independent flowers which have undergone phylogenetic fusion. This is also amply evidenced by floral anatomy.

The above interpretations further lead to the problem whether the pistil is appendicular or axial. Vascular anatomy shows that there is nowhere in the ovary a residual trace or an axis around which carpels are arranged. The vascular elements are completely used up by the differentiated carpels. It is on this basis that flowers of Saururaceae have been interpreted as condensed inflorescence of the "sympodial type" simulating to a considerable extent vegetative branches where sympodial growth prevails. Anatomical evidences do not, however, give a correct picture of inferior ovary. Developmental studies are necessary for the interpretation of inferior ovary in some members of Saururaceae.

The trends of specialization postulated by Bailey and Swamy (1951) for the ranalian carpel have recently been useful in interpreting some primitive carpels. Although carpels of *Houttuynia* and *Anemopsis* are quite specialized, the conduplicate nature is still present in their styles which have flared-out stigmatic crests.

Although ontogenetic studies have not been made, available observations indicate that the ovule-bearing capacity of the carpel has brought several modifications in its train. The closure of carpels has occurred in the basal or ovule-bearing part leaving behind an extensive stigmatic crest. The stigmatic crest is supplied by both dorsal and ventral bundles. This feature is seen in *Saururus, Houttuynia* and *Anemopsis*. In some of the carpels, particularly of S. *cernuus*, retraction of ventral traces from stigmatic region toward the ovule-bearing part may be noticed. This retraction leaves a short style between ovary and stigma. In the case of S. *chinensis*, the stigmatic crest is supplied by both ventral and dorsal traces; it is situated just above the ovule-bearing part. This progressive phylogenetic specialization leading to the formation of a style between stigma and ovary is exhibited by the carpels of *Saururus, Houttuynia* and *Anemopsis*.

Superimposed on the evolutionary specialization mentioned above there is concomitant lateral concrescence of carpels resulting in a compound pistil. Furthermore, the "spiral" arrangement of carpels becomes less and less clear. Thus, in the development of pistils, simple or compound, several independent trends of specialization have occurred simultaneously in the Saururaceae.

Placentation in the Saururaceae is of two types, laminar and parietal. Laminar placentation is found in *Saururus* and parietal placentation in *Houttuynia* and *Anemopsis*. Bailey and Swamy (1951) after an extensive survey of carpels in the Ranales have come to the conclusion that carpels with laminar placentation are primitive and show various trends of specialization leading toward other types of placentation. A detailed study of carpels of *Saururus* has shown not only a laminar placentation but also different degrees of incipient syncarpous tendencies. The carpellary margins undergo concrescence or close approximation. This concrescence of carpellary margins does not occur at one level since they are arranged spirally. Axial tissue that is seen at the base of carpels is actually a composite of different carpellary margins. As a consequence, the pistil appears to be compound with more than one locule. In fact, this condition probably led several taxonomists to interpret this placentation as axile (Bailey, 1958; Lawrence, 1951; Benson, 1957).

From this basic laminar placentation, parietal placentation of *Houttuynia* and *Anemopsis* can be derived. The presence of free styles in the pistils of the above two genera shows that lateral concrescence of adjacent carpels has occurred in the ovule-bearing parts of carpels. Closely approximated partitions appear in the locule of the ovary of *Houttuynia* and *Anemopsis*. These partitions are the fused ventral carpellary margins. In the ovule bearing part, ventral parts of carpels have been retracted considerably apparently to accommodate the ovules developing inside.

In the organization of syncarpous ovary from simple carpels in Saururaceae, the so-called classical "torus" is not involved. The evolutionary trend of specialization from laminar to parietal placentation involves: firstly, the fusion of ventral margins of adjacent carpels; and secondly, lateral concrescence of the same carpels. These are further influenced greatly by the ovule bearing capacity of a syncarpous ovary. In *Houttuynia* and *Anemopsis* the ovary becomes "multilocular". The

retraction of partitions within the ovary in the lower part may be due to the acquisition of ovule-bearing capacity of ovary. Normally, the ovaries of genera mentioned above show multilocular nature in the upper part of ovary and unilocular in the lower part. Intermediate conditions showing various stages of phylogenetic retraction of partitions are not infrequent.

Eichler (1875-78) interpreted the flowers of *Saururus* and *Houttuynia* as obdiplostemonous; flowers which had two whorls of three stamens each and the outer whorl had aborted. In the present investigation the above-said feature has not been observed. In *Anemopsis* and *Gymnotheca*, each flower is usually associated with six stamens. Anatomy of flower has shown that traces for stamens arise from the dorsal bundle of carpels. In addition to the above feature, the first formed carpels of *Saururus* usually possess two stamens each, the last formed does not develop stamens. The absence of correlation between the number of carpels and stamens, negates the possibility of recognizing two whorls of stamens. A similar view has also been advanced by Nozeran (1955).

In his comparative survey of floral structures Nozeran (1955) writes that "the spike of *Houttuynia* is not entirely an inflorescence and is not still a flower". Furthermore, he hypothesized that the lowermost bracts transform into perianth lobes. He also observed in inflorescence several instances of reduction in number of stamens and carpels. On the basis of above details, he derived the spike of *Houttuynia* from a homogeneous inflorescence which was composed probably of trimerous flowers. In the present investigation, however, all the details given by Nozeran (1955) were not found. There is no doubt that at the tip of the inflorescence, an overy was often borne, but there has not been enough evidence at present to support Nozeran's hypothesis.

Embryological investigations show great similarities among the three species, *Saururus cernuus*, *Houttuynia cordata* and *Anemopsis*. Development of both male and female gametophytes are very similar. During development of female gametophyte the archesporial cell gives rise to parietal cells in *Saururus* and *Anemopsis*. These parietal cells are absent in *Houttuynia*. The development of the female gametophyte in all three species studied conforms to the monosporic type (as here interpreted). Some stages in the development of endosperm were observed in *Houttuynia* and *Saururus cernuus*. In both cases the endosperm is of the cellular type. The above two genera also show endosperm haustoria. The embryo in *S. cernuus* suggests that the first division of the zygote should be transverse. Seeds enclose a massive perisperm and a little endosperm surrounding the small embryo. Similar embryological features have been recorded by Johnson (1900) for *S. cernuus*.

Summary

An account of floral anatomy and embryology suggests that the genera of Saururaceae are closely interrelated. Structure and morphology of inflorescence and flower are discussed in the light of anatomy.

Anatomical details indicate that the inflorescence-type seen in *Anemopsis* is more specialized than the type seen in *Saururus* or other genera. This has been

achieved, according to the evidences advanced, by processes of reduction, adnation and cohesion of various floral entities.

Some of the morphological aspects of ovary, carpels and placentation have been discussed. Embryological details are similar in all the genera investigated here.

Acknowledgements

I am greatly indebted to Dr. N. H. Nickerson, for his kindness and generosity and valuable guidance during the course of this investigation. I am also highly thankful to Dr. R. E. Woodson, Jr., for generously placing some of the material used here at my disposal and for helpful suggestions.

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HEPATICITES DEVONICUS
A NEW FOSSIL LIVERWORT FROM THE DEVONIAN OF NEW YORK[1,2]

FRANCIS M. HUEBER

Abstract

Hepaticites **devonicus** is described from the lowermost Upper Devonian of New York. Many fragments were obtained by macerating shale This is the oldest fossil hepatic reported to date. It is tentatively considered to be a member of the Anacrogynae, and is compared with the living genera *Pallavicinia* and *Metzgeria*. FRANCIS M. HUEBER, Department of Botany, Cornell University, Ithaca, New York.

Introduction

The record of the Hepaticae in the Paleozoic is very meager. One may readily expect this to be the case owing to the small size and the delicate nature of the members of this group of plants. Up until now the oldest occurrence of undoubted hepatics was that of four species from the Upper Carboniferous of Shropshire, England (Walton, 1925, 1928). They are *Hepaticites Kidstoni, H. lobatus, H. Langi* (Walton, 1925), and *H. Metzgerioides* (Walton, 1928). These four fossil forms have been compared with the living genera *Treubia, Fossombronia, Riccardia* (*Aneura*) and *Metzgeria* respectively. In all cases the remains are of sterile shoots only and on the basis of their morphology it has been assumed that all of the forms are of the anacrogynous series of the Jungermanniales (Walton, 1925, 571). Definite conclusions can not be made until reproductive organs are found.

Materials and Methods

The plant remains which are described here occur as compressions associated with other plant remains in a fine-grained, dark-gray shale. The specimens were collected from a small quarry located on the northwest slope of South Mountain, Schoharie County, New York, 1.1 miles west of the Schoharie–Greene County line Livingston 7′ 30″ map at 74° 16′ 30″ E., 42° 23′ 55″ N. and at an elevation of 2180 feet. The horizon at which the quarry is located is very close to the base of the Onteora "red beds" which are the continental equivalent to the lowermost two-thirds of the marine Finger Lakes stage, Senecan series (Frasnian) of central and western New York. The beds are therefore lowermost Upper Devonian.

The plants with which the specimens of *Hepaticites* are associated, that is in the same beds and at the same quarry, are *Psilophyton princeps* Dawson 1871, *Schizopodium* Harris 1929, *Cladoxylon* Unger 1856, *Pseudosporochnus* Potonie and Bernard 1904, *Eospermatopteris* (Dawson) Goldring 1924, *Callixylon* Zalessky 1911, and two new genera all of which are to be described in future papers.

While preparing transfers of other plant remains, thin fragments of plant material were seen in the sludge derived from the dissolution of the shale. The fragments at first were thought to be epidermal layers from plants contained in the shale. However, after they were washed, dehydrated and mounted, they were

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[1] This paper is a part of a thesis presented to the Graduate School of Cornell University in partial fulfillment of the requirements for the Ph.D. degree.

[2] Communicated by Henry N. Andrews.

found to possess the characteristics of the genus *Hepaticites*. Additional preparations were made using the bulk maceration technique (Harris, 1926). Pieces of rock in which large quantities of plant remains are evident are placed into polyethylene or polystyrene plastic containers. Concentrated hydrofluoric acid (48%) is poured over the specimens until they are completely immersed in the acid. From ten to twenty-four hours are generally required for dissolution of the rock; the time is of course dependent upon the size of the specimen being dissolved. Frequent observations of the progress of the reaction are necessary in order that any freed plant material which is either floating on the surface of the acid or lying in the sludge can be removed. The remains are easily removed by slipping a flat, wooden rod under the specimen and then carefully raising the rod out of the solution. The specimen is "floated" onto the rod in the way that one floats specimens of algae onto paper for the preparation of herbarium sheets. The writer has found that the wooden labels used for flower pots are very satisfactory for lifting the specimens from the solution. The plant material is floated off of the rod into a container of water and washed through three or four changes of water. The wash water is either decanted or siphoned off. After the specimen is washed, it is floated onto a glass slide and positioned on the slide by the use of brushes cut down to a single bristle. The slide is gradually raised from the water, keeping the slide inclined. A drop or two of liquid detergent added to the water will help reduce surface tension and facilitate the removal of the specimen. Any water remaining on the slide and around the specimen is carefully removed with blotting paper. After the specimen has partially dried, it is saturated with a 1% aqueous solution of gum arabic which when dried serves to hold the specimen in place on the surface of the slide. The gum arabic solution is applied with a fine-tipped brush. When the specimen is fully dried, a drop of Harleco Synthetic Mounting Medium or Canada balsam dissolved in xylene is placed on top of it and a coverslip lowered over the surface. At this point, if the specimen were not fixed to the surface of the slide with gum arabic, it would migrate to the edge of the coverslip or be broken by the flow of the viscous mounting medium. The mounting medium is dried and the preparation is ready for study. Nearly eighty fragments were prepared in this way.

Genus HEPATICITES Walton 1925

Hepaticites **devonicus** sp. nov.—Description

The thallus is very simply differentiated into two parts, a rhizomatous portion and a thallose region. The latter is differentiated into two parts, an axial or costal region composed of elongate parenchymatous cells and marginal wings or lamellae composed of polygonal parenchymatous cells (figs. 1–5). The axial region averages 0.56 mm. in width. It is two to several cells thick; the actual number is impossible to determine because of the complex reticulum formed by the outlines of the cells. A midrib composed of very elongate cells and averaging 0.22 mm. in width forms the central portion of the axial region. The midrib is in turn surrounded by a zone of elongate cells which are transitional in size between the midrib and the cells of the wings. The cells are elongate parallel to the long axis of the thallus and are 14 to 26 μ in diameter. Because of the incomplete preserva-

tion of the end walls, the full length of any one of the cells of the midrib is unknown. The cells which form the transition zone between the midrib and the wings average 140 μ in length. No rhizoids are evident along the axial region. The wings are only one cell thick and vary from 1.3 to 1.75 mm. in width. The cells are 46.8 to 73.2 μ in diameter and are polygonal in outline. Scattered through the tissue of the wings are dark cells (fig. 5). The contents may indicate that some of them were storage or secretory cells. Some, however, may be darkened due to the activity of fungi, for fungal hyphae are commonly observed adhering to the surfaces of the thallus. The margins of the wings are serrate, the teeth are spaced at intervals of 0.18 mm. (figs. 6, 7), but otherwise the margins show no well pronounced lobing. Dichotomous branching of the thallus is evidenced in three specimens, two of which are illustrated in figs. 2 and 3. Fragments of the wings are still attached to the axial regions beyond the dichotomy. Growth of the plant was apparently the result of the divisions of a single apical cell borne in a notch at the apex of the thallus. A fragment of the thallus illustrating what may be interpreted as an example of the apical notch is shown in fig. 4.

The rhizomatous portion of the plant (fig. 8) varies from 0.58 to 1.7 mm. in width and is composed wholly of elongate parenchymatous cells. The midrib varies from 0.15 to 0.28 mm. in width; the cells of which it is composed vary from 14 to 29 μ in diameter and as in the midrib of the thallus portion their length is unknown. The cells which surround the midrib are approximately the same diameter as those in the midrib and they vary from 136 to 220 μ in length. Numerous rhizoids arise from the cells on the surface of the rhizome (figs. 8 and 9). They are nonseptate and average 21 μ in diameter just above the broadened base. The tips of the rhizoids are broken off and therefore the full length of any one individual is not known. The largest fragment is 0.56 mm. in length. It must be stated here that no rhizomatous portion has been found in direct organic connection with the thallose portion of the plant. Both parts were isolated from the same matrix and since the part which is here referred to as the rhizome has the same general form and structure of the axial region of the thallose segment, the writer feels justified in considering them parts of the same plant.

Discussion

A comparsion of the illustrations of *Hepaticites devonicus* with those for the species *H. Metzgerioides* (Walton, 1928, Plate XII, Figs. 1–6) will show how similar the thallose portion of *H. devonicus* is to one which has already been included in the genus *Hepaticites*. The finely serrate margin, the lack of rhizoids on the thallose portion of the plant, and the differentiation of a rhizome bearing rhizoids, all characteristics of *H. devonicus*, are the evident morphological differences between the two species. The difference in the gross size between the two (*H. devonicus* is perhaps four to five times larger than *H. Metzgerioides*) may be of specific value, but the similar size of the constituent cells in the two plants suggests that the difference is probably one of growth form.

As in *H. Metzgerioides*, *H. devonicus* shows a clear distinction between midrib and wing which is also characteristic of the modern genera *Pallavicinia* Gray, corr. Carruthers and *Metzgeria* Raddi. *Hepaticites devonicus* combines characteristics

of both of the modern genera. It is similar to *Pallavicinia* in the width of the thallus (3 to 4 mm.) and may represent a plant like *Pallavicinia Zollingeri* (Gottsch.) Schiffn. (See Smith, 1938, especially Fig. 32 and Campbell and Williams, 1914, especially Fig. 4) in which there is differentiation of a prostrate portion bearing rhizoids and an erect, branched portion on which rhizoids are not present. The small marginal teeth of the thallus in *H. devonicus* is another character which is shared with *Pallavicinia Zollingeri*. *Hepaticites devonicus* differs from *Pallavicinia* in having a less differentiated central strand and larger central cells in the strand. *Hepaticites devonicus* and *Metzgeria* are similar in their slightly differentiated central strands, in the size of the cells in the central strand, the size of the cells in the wings, and the possibility that the teeth on *H. devonicus* are homologous to the hairs on the margins of the thallus in *Metzgeria*. They differ in that *Metzgeria* is smaller (1 to 2 mm. wide) and bears rhizoids along its midrib. *Hepaticites devonicus* resembles *Metzgeria* in cellular details but resembles *Pallavicinia* in size and form.

Reproductive structures are not known for *H. devonicus* but on the basis of its similarity in habit and the many details of structure which it shares with members of the Anacrogynae the writer suggests that it be classed with this group until such a time as further evidence of its relationship is obtained.

The occurence in Devonian sediments of remains assignable to the genus *Hepaticites* extends the range of the Hepaticae even further back in geologic time, and it emphasizes that this class of plants had evolved to a high order of organization far earlier than heretofore recorded.

Hepaticites **devonicus** Hueber sp. nov.

Diagnosis: Dichotomously branching thallus differentiated into rhizomatous portion bearing rhizoids and thallose portion composed of axial region averaging 0.56 mm. in diameter and wings one cell in thickness ranging from 1.3 to 1.75 mm. in width. Cells of the axial region elongate, 14 to 26 μ in diameter, length of central cells undetermined, length of transitional cells averaging 140 μ. Cells of the wings polygonal, 46.8 to 73.2 μ in diameter. Margins of wings finely serrate, lobing indefinite. Rhizomatous portion 0.58 to 1.7 mm. in diameter, cells elongate as in axial region of thallose portion, numerous non septate rhizoids averaging 21 μ in diameter borne on surface of rhizome.

Holotype number 23, specimen 1579-294, slides 6–12, paleobotanical collections of the Department of Botany, Cornell University, New York.

Locality: Northwest slope South Mountain, Schoharie County, New York.

Horizon: Base of the Onteora "red beds" lowermost Upper Devonian.

Summary

A new species of *Hepaticites, H. devonicus*, is described from the lowermost Upper Devonian of New York. The plant is differentiated into two parts, a rhizomatous portion and a thallose region. The latter is differentiated into two parts, an axial region composed of elongate parenchymatous cells and marginal wings which are one cell thick and composed of polygonal parenchymatous cells.

The margins of the wings are finely serrate and show no lobing. There are no rhizoids borne on the thallose portion of the plant. The rhizome is composed wholly of elongate parenchymatous cells and resembles the axial region of the thallose portion of the plant. Rhizoids occur over the entire surface of the rhizome. No reproductive structures are known.

The plant is compared with *Pallavicinia Zollingeri* and *Metzgeria* and placed for the time being with the fossil forms of the Anacrogynae.

The report constitutes the earliest record of the Hepaticae in the geologic column.

Acknowledgements

The writer wishes to express his sincere appreciation to Dr. Harlan P. Banks for his supervision and guidance during the course of the research which resulted in the discovery of a diverse flora in the Devonian of eastern New York. Special acknowledgement is extended to the National Science Foundation for the support afforded by graduate fellowships for the years 1957-1958, 1958-1959 and 1959-1960 during which time the research was carried to completion. Thanks are extended to Dr. Rudolph Schuster for his suggestions concerning the specimens of *Hepaticites* and to Mrs. J. Douglas Grierson for the photographic prints used to illustrate the present paper.

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Explanation of Plate

PLATE I

Hepaticites devonicus

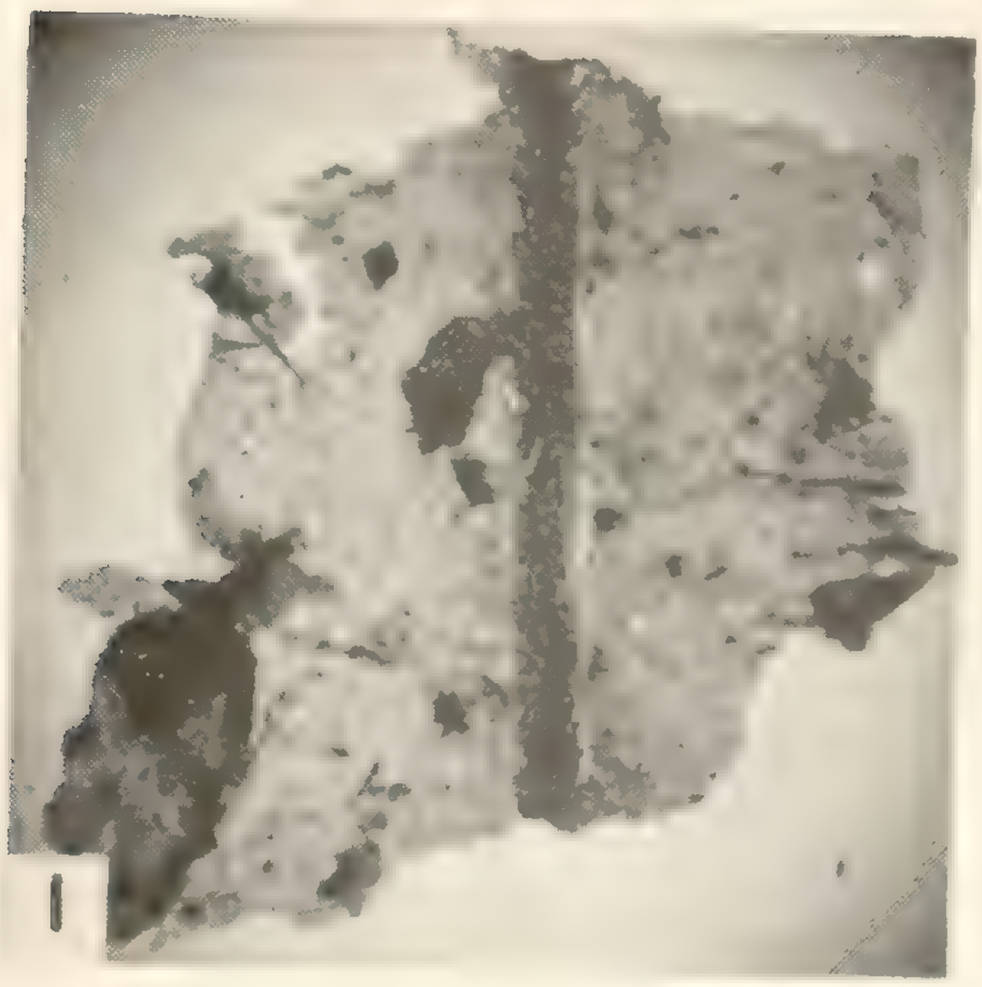
Fig. 1. Portion of the thallose region of the plant showing the differentiation of the axial region and the marginal wings. Slide 12, × 9.

Fig. 2. Portion of the thallose region of the plant showing a dichotomy of the axis. Note the elongate cells of the axial region and the polygonal cells of the marginal wings. Slide 8, × 29.

Fig. 3. Portion of the thallose region of the plant showing a dichotomy of the axis. The marginal wings are folded over the midrib in upper portions of the specimen. Slide 9, × 7.

Fig. 4. Apex of the thallose portion of the plant. Slide 11, × 58.

Fig. 5. Detail of the marginal wing of the thallose portion of the plant. Note the darkened cells which may have been storage or secretory cells. Slide 10, × 78.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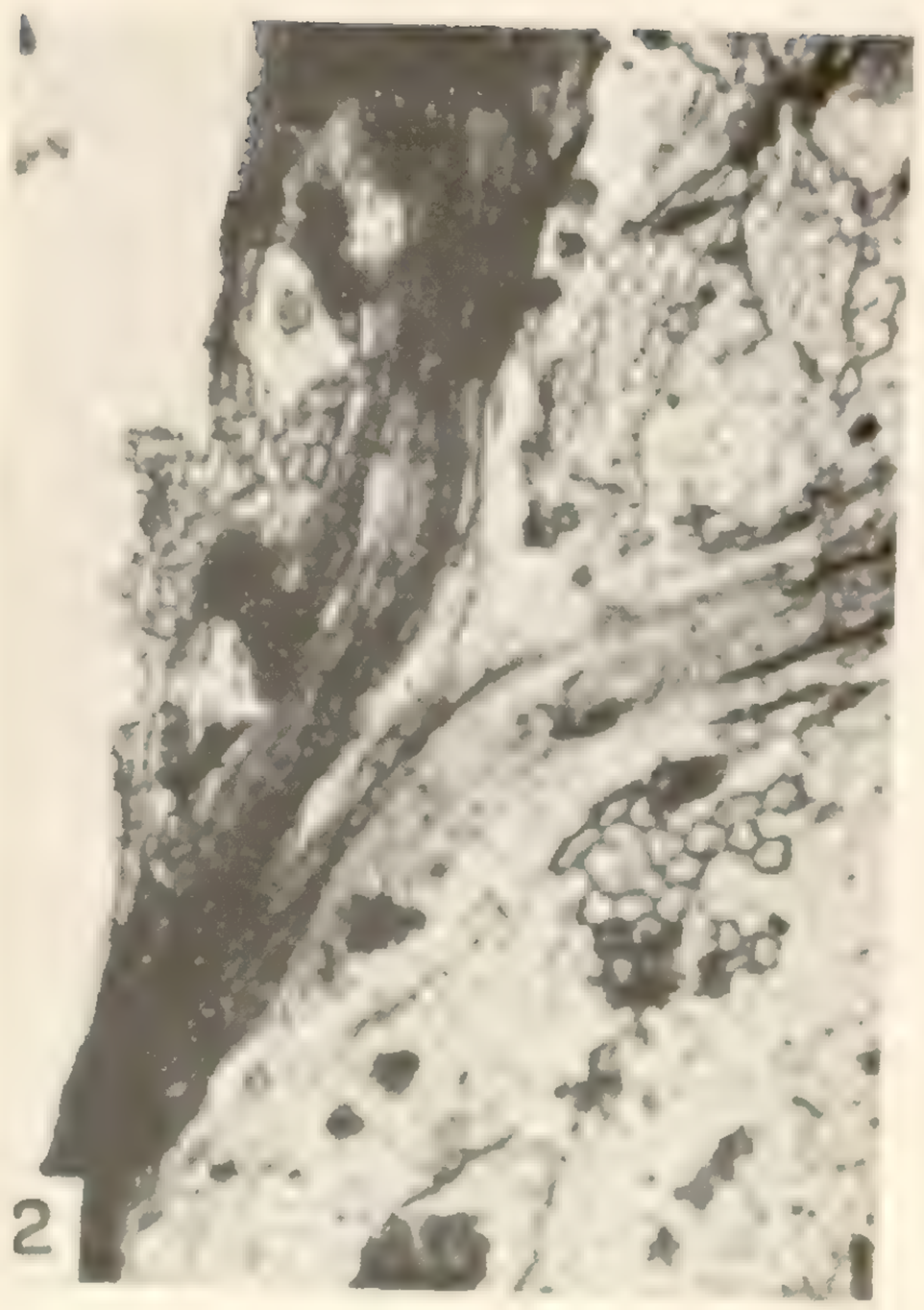
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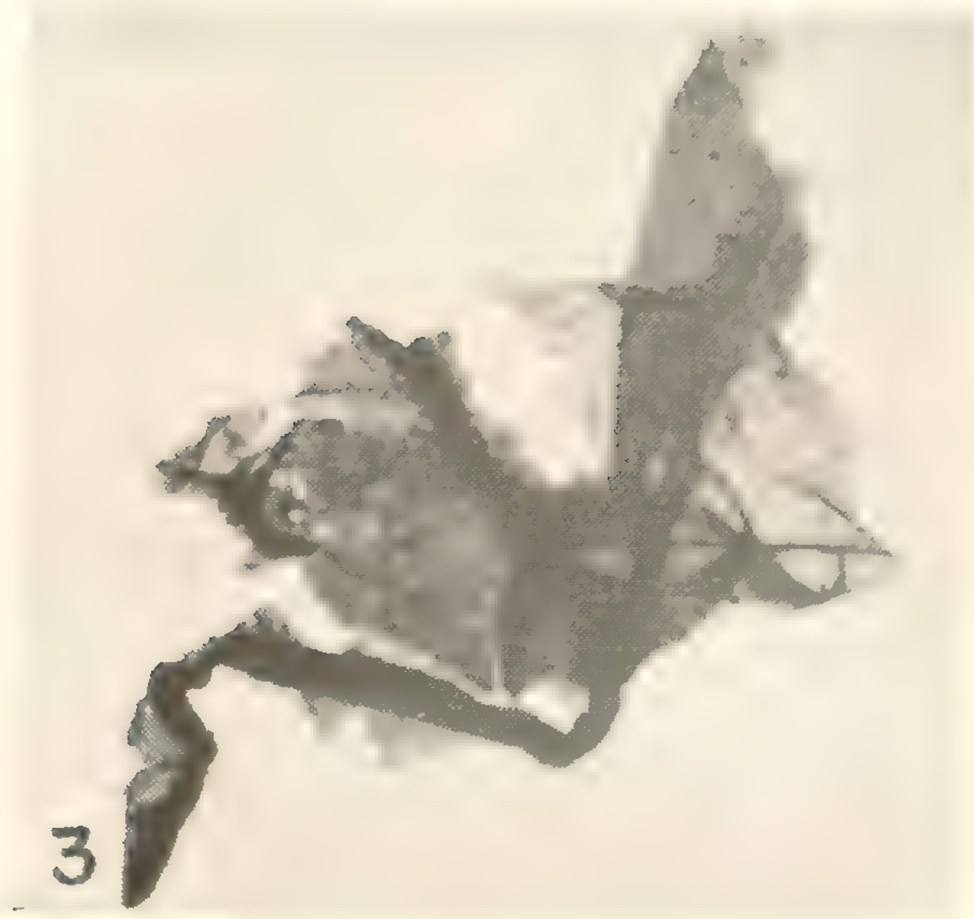
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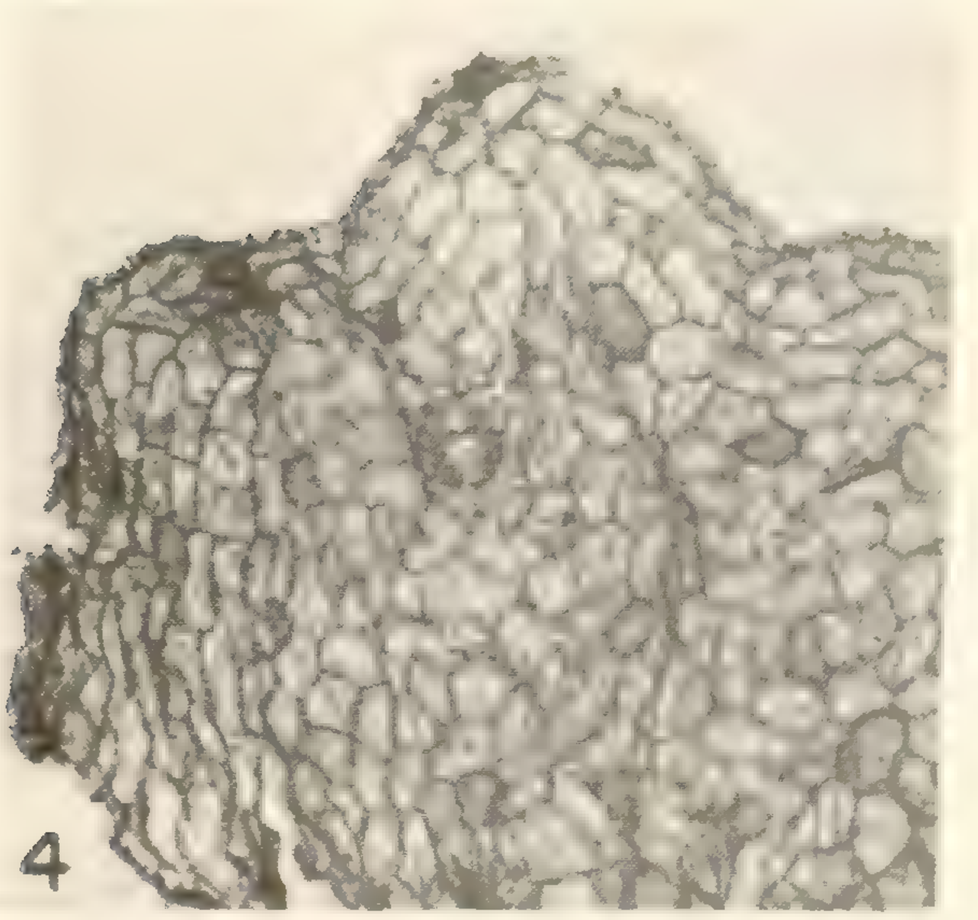
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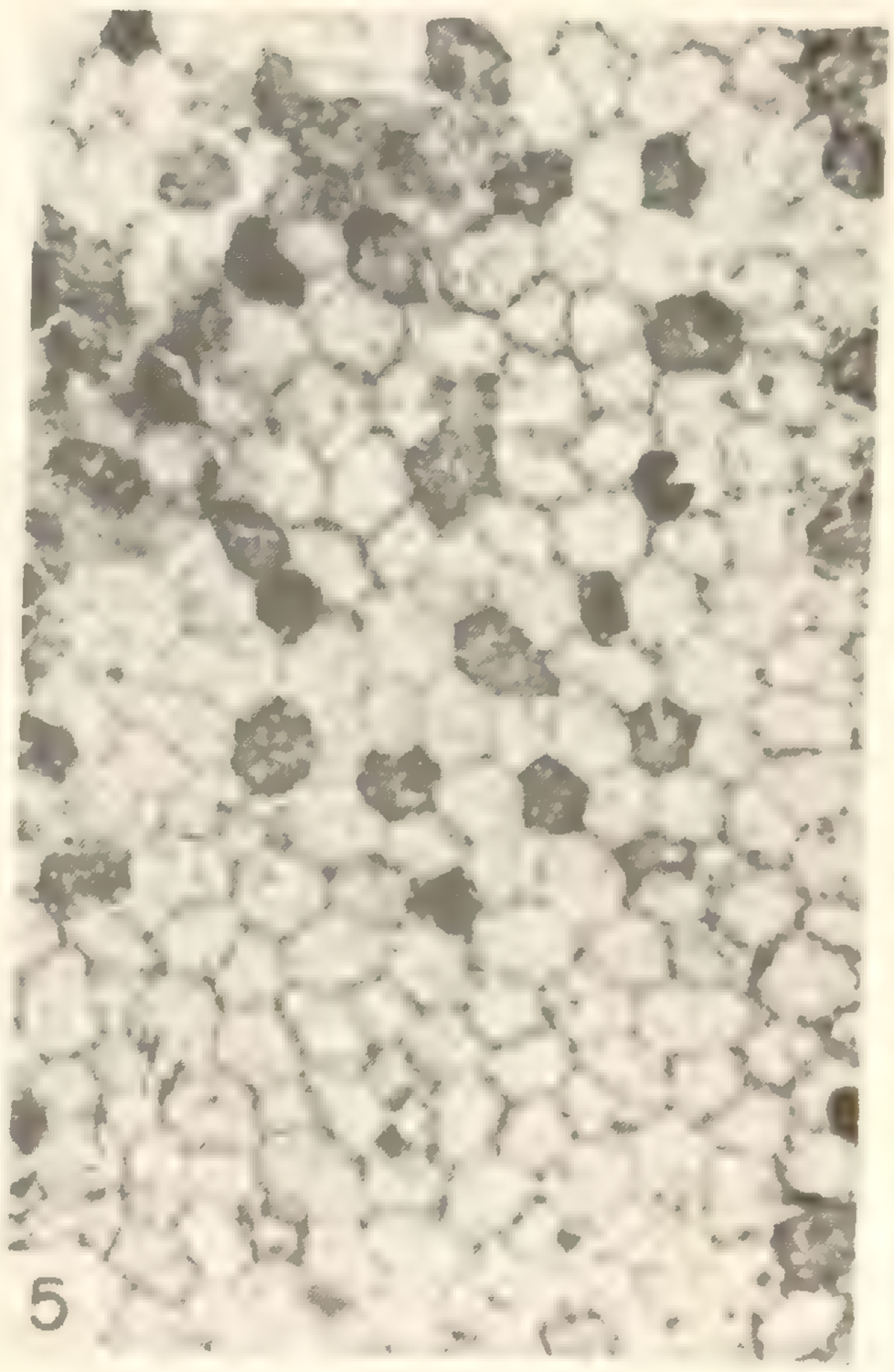
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HUEBER—HEPATICITES DEVONICUS

HUEBER—HEPATICITES DEVONICUS

Explanation of Plate

PLATE II

Hepaticites devonicus

Fig. 6. Portion of the marginal wing of the thallose region of the plant illustrating the serrate margin of the wing. Slide 7, × 27.

Fig. 7. Detail of one of the marginal teeth shown on the specimen in Fig. 6. Slide 7, × 205.

Fig. 8. Fragment of the rhizomatous portion of the plant. Note the dense covering of nonseptate rhizoids. Slide 6, × 16.

Fig. 9. Detail of the surface of the rhizomatous portion of the plant showing the broad bases of the rhizoids. The tips of the rhizoids are broken off. Slide 6, × 190.

INDEX OF ORCHID NAMES — 1960

ROBERT L. DRESSLER

As an aid to ourselves and others studying the orchids, we have started an index of new orchid names, to be published annually. It is felt that such an index may be of value to the many botanists and others interested in this large and complex family. For new taxa we have indicated the country or origin and the location of type material (using the standard abbreviations), if this is known. For new combinations, new names or changes in rank, we cite the basionym with the new name. We have abbreviated the authors' names less than is customary, as we feel that a saving of only one or two spaces does not justify the loss of clarity. A few names which were published in mimeographed news letters are purposely omitted. Such publication is of dubious validity under the rules of nomenclature, and certainly should be avoided. We would be very glad to receive corrections or additions to the index, to be appended to the Index for 1961.

Subfamily **Cypripedioideae** Garay, Bot. Mus. Leafl. 19:86. Type genus: *Cypripedium* L.

Subfamily **Epidendroideae** Dressler, Taxon 9:213. Based on *Kerosphaeroideae* Garay.

Subfamily **Kerosphaeroideae** Garay, Bot. Mus. Leafl. 19:87. Type genus: *Epidendrum* L. This name is not legitimate under the Rules of Nomenclature.

Subfamily **Neottioideae** Garay, Bot. Mus. Leafl. 19:86. Type genus: *Neottia* Sw.

Subfamily **Ophrydoideae** Garay, Bot. Mus. Leafl. 19:87. Type genus: *Orchis* L. This name is not legitimate under the Rules of Nomenclature; this subfamily must be known as the Orchidoideae.

Aeranthes **albidiflora** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 205. Madagascar (TAN).

Aeranthes **ambrensis** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 209. Madagascar (TAN).

Aeranthes **carnosa** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 209. Madagascar (TAN).

Aeranthes **denticulata** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 207. Madagascar (TAN).

Aeranthes **neoperrieri** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 212. Madagascar (TAN).

Aeranthes **orthopoda** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 212: Madagascar (TAN).

Bletia purpurea var. **alba** Ariza-Julia & Jiménez, Rhodora 62:236. Dominican Republic.

Bulbophyllum jacquetii var. **rosea** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32: 189. Annam (P?).

Bulbophyllum **rugosibulbum** Summerh., Kew Bull. 14:138. Northern Rhodesia (K).

Cephalantheropsis lateriscapa Guillaumin, Bull. Mus. Hist. Nat. Paris II 32: 188–189. Annam (P?).

Chroniochilus **virescens** (Ridley) Holttum, Kew Bull. 14:273. *Sarcochilus virescens* Ridley.

Cleisostoma **tixieri** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32:369. Annam (P?).

Cypripedium × *andrewsii* nm. **favillianum** (J. T. Curtis) Boivin, Naturaliste Canadien 87:32. *Cypripedium* × *favillianum* J. T. Curtis.

Cypripedium × *andrewsii* nm. **landonii** (Garay) Boivin, Naturaliste Canadien 87: 32. *Cypripedium* × *landonii* Garay.

Cyrtorchis arcuata ssp. **leonensis** Summerh., Kew Bull. 14:149. Sierra Leone (K).

Cyrtorchis arcuata ssp. **variabilis** Summerh., Kew Bull. 14:148. Tanganyika Terr. (K).

Cyrtorchis arcuata ssp. **whytei** (Rolfe) Summerh., Kew Bull 14:147. *Listrostachys whytei* Rolfe.

Cyrtorchis **neglecta** Summerh., Kew Bull. 14:149. Tanganyika Terr. (K.)

Dactylorhiza—Soó (Ann. Univ. Scient. Budapest. Eötvös Biol. 3:335–357) gives a synopsis of *Dactylorhiza* (*Dactylorchis*) which includes many apparent new combinations for species, subspecies and hybrid populations. We do not list these here because there is not "a full and direct reference to its author and original publication" with the basionyms. Further, it is quite unclear just which names Soó intends to publish as new combinations. It seems unlikely that one would intentionally publish so many new combinations in *Dactylorhiza* while recommending that *Dactylorchis* be considered for conservation.

Diaphananthe section **Rhipidoglossum** (Schltr.) Summerh., Kew Bull. 14:141. *Rhipidoglossum* Schltr.

Diaphananthe **brevifolia** (Summerh.) Summerh., Kew Bull. 14:143. *Rhipidoglossum brevifolium* Summerh.

Diaphananthe **cuneata** Summerh., Kew Bull. 14:141. Uganda (K).

Diaphananthe **densiflora** (Summerh.) Summerh., Kew Bull. 14:143. *Rhipidoglossum densiflorum* Summerh.

Diaphananthe **erecto-calcarata** (De Wild.) Summerh., Kew Bull. 14:143. *Angraecum erecto-calcaratum* De Wild.

Diaphananthe **globoso-calcarata** (De Wild.) Summerh., Kew Bull. 14:142. *Angraecum globoso-calcaratum* De Wild.

Diaphananthe **laxiflora** (Summerh.) Summerh., Kew Bull. 14:141. *Rhipidoglossum laxiflorum* Summerh.

Diaphananthe **longicalcar** (Summerh.) Summerh., Kew Bull. 14:142. *Rhipidoglossum longicalcar* Summerh.

Diaphananthe **microphylla** (Summerh.) Summerh., Kew Bull. 14:142. *Rhipidoglossum microphyllum* Summerh.

Diaphananthe **obanensis** (Rendle) Summerh., Kew Bull. 14:142. *Angraecum obanense* Rendle.

Diaphananthe **peglerae** (Bolus) Summerh., Kew Bull. 14:143. *Mystacidium peglerae* Bolus.

Diaphananthe **rohrii** (Reichb. f.) Summerh., Kew Bull. 14:140. *Angraecum rohrii* Reichb. f.

Diaphananthe **rutila** (Reichb. f.) Summerh., Kew Bull. 14:143. *Aëranthus rutilus* Reichb. f.

Diaphananthe **xanthopollinia** (Reichb. f.) Summerh., Kew Bull. 14:143. *Aëranthus xanthopollinius* Reichb. f.

Dinklageëlla **minor** Summerh., Kew Bull. 14:156. Liberia (K).

Epidendrum **hioramii** Acuña & Alain, Mem. Soc. Cubana Hist. Nat. 24:110. Cuba (SV).

Epipactis thunbergii forma **subconformis** Sakata, Jour. Jap. Bot. 35:224. Japan (Herb. T. Sakata).

Eulophia **laurentii** (De Wild.) Summerh., Kew Bull. 14:139. *Lissochilus laurentii* De Wild.

Habenaria section **Kryptostoma** Summerh., Kew Bull. 14:135. Type species: *H. tentaculigera* Reichb. f.

Habenaria **gonatosiphon** Summerh., Kew Bull. 14:134. Tanganyika Terr. (K).

Habenaria **magnirostris** Summerh., Kew Bull. 14:132. Tanganyika Terr. (K).

Habenaria **richardsiae** Summerh., Kew Bull. 14:131. Tanganyika Terr. (K).

Holothrix **brachycheira** Summerh., Kew Bull. 14:127. Northern Rhodesia (K).

Holothrix **papillosa** Summerh., Kew Bull. 14:128. Tanganyika Terr. (K).

Holothrix **pentadactyla** (Summerh.) Summerh., Kew Bull. 14:129. *Deroemera pentadactyla* Summerh.

Laeliopsis domingensis var. **alba** Ariza-Julia & Jiménez, Rhodora 62:236. Dominican Republic.

Luisia **acutilabris** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32:188. Laos (P?).

Masdevallia **horrida** Teuscher & Garay, Amer. Orchid Soc. Bull. 29:23. Costa Rica (AMES).

Maxillaria imbraicata var. **carinata** (Rodr.) Pabst, Orquidea (Brazil) 22: 134. *Maxillaria carinata* Rodr.

Maxillaria imbricata var. **iguapensis** (Hoehne & Schltr.) Pabst, Orquidea (Brazil) 22: 134. *Maxillaria iguapensis* Hoehne & Schltr.

Oberonia **attenuata** Dockrill, No. Queensland Naturalist 29:4. Australia (BRI).

Oberonia recurva var. **lingmalensis** (Blatt. & McC.) Sant. & Kapadia, Jour. Bombay Nat. Hist. Soc. 57:259. *Oberonia lingmalensis* Blatt. & McC.

Oberonia **santapaui** Kapadia, Jour. Bombay Nat. Hist. Soc. 57:265. *Oberonia lindleyana* Wight, 1851, not *O. lindleyana* Duperr., 1834.

Oberonia **trullaelabris** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32:115. Annam (P?).

Orchis rotundifolia forma **beckettii** Boivin, Naturaliste Canadien 87:42. Canada (DAO).

Peristylus **densus** (Lindley) Santapau & Kapadia, Jour. Bombay Nat. Hist. Soc. 57:128. *Coeloglossum densum* Lindley.

Polystachya **bella** Summerh., Kew Bull. 14:137. Kenya Colony (K).

Polystachya **testuana** Summerh., Kew Bull. 14:136. Gabon (Herb. Le Testu).

Pteroceras **alatum** (Holttum) Holttum, Kew Bull. 14:269. *Sarcochilus alatum* Holttum.

Pteroceras **appendiculatum** (Bl.) Holttum, Kew Bull. 14:269. *Dendrocolla appendiculata* Bl.

Pteroceras **berkeleyi** (Reichb. f.) Holttum, Kew Bull. 14:269. *Thrixspermum berkleyi* Reichb. f.

Pteroceras **biserratum** (Ridley) Holttum, Kew Bull. 14:269. *Sarcochilus biserratus* Ridley.

Pteroceras **caligare** (Ridley) Holttum, Kew Bull. 14:269. *Sarcochilus caligaris* Ridley.

Pteroceras **carrii** (L. Wms.) Holttum, Kew Bull. 14:269. *Sarcochilus carrii* L. Wms.

Pteroceras **ciliatum** (Ridley) Holttum, Kew Bull. 14:269. *Dendrocolla ciliata* Ridley.

Pteroceras **compressum** (Bl.) Holttum, Kew Bull. 14:270. *Dendrocolla compressa* Bl.

Pteroceras **ecalcaratum** (Holttum) Holttum, Kew Bull. 14:270. *Sarcochilus ecalcaratus* Holttum.

Pteroceras **emarginatum** (Bl.) Holttum, Kew Bull. 14:270. *Dendrocolla emarginata* Bl.

Pteroceras **fasciculatum** (Carr) Holttum, Kew Bull. 14:270. *Sarcochilus fasciculatus* Carr.

Pteroceras **hirsutum** (Hooker f.) Holttum, Kew Bull. 14:270. *Sarcochilus hirsutus* Hooker f.

Pteroceras **johorense** (Holttum) Holttum, Kew Bull. 14:270. *Sarcochilus johorensis* Holttum.

Pteroceras **minutiflorum** (Ridley) Holttum, Kew Bull. 14:270. *Asochilus minutiflorus* Ridley.

Pteroceras **pallidum** (Bl.) Holttum, Kew Bull. 14: 270. *Dendrocolla pallida* Bl.

Pteroceras **siamense** (Ridley) Holttum, Kew Bull. 14:271. *Asochilus siamensis* Ridley.

Pteroceras **stenoglottis** (Hooker f.) Holttum, Kew Bull. 14:271. *Sarcochilus stenoglottis* Hooker f.

Pteroceras **sauveolens** (Roxb.) Holttum, Kew Bull. 14:271. *Aërides suaveolens* Roxb.

Pteroceras **tanyphyllum** (Ridley) Holttum, Kew Bull 14:271 *Sarcochilus tanyphyllus* Ridley.

Pteroceras **teres** (Bl.) Holttum, Kew Bull. 14:271. *Dendrocolla teres* Bl.

Pteroceras **teysmannii** (Miq.) Holttum, Kew Bull. 14:271. *Aërides teysmannii* Miq.

Pteroceras **violaceum** (Ridley) Holttum, Kew Bull. 14:272. *Sarcochilus violaceus* Ridley.

Pteroceras **viridiflorum** (Thw.) Holttum, Kew Bull. 14:272. *Aërides viridiflora* Thw.

Pteroceras **zollingeri** (Reichb. f.) Holttum, Kew Bull. 14:272. *Dendrocolla zollingeri* Reichb. f.

Schizochilus **lepidus** Summerh., Kew Bull. 14:130. Mozambique (Southern Rhodesia Gov. Herb.).

Schomburgkia × **parkinsoniana** H. G. Jones, Jour. Barbados Mus. Hist. Soc. 28: 4. Barbados (parent species introduced).

Thrixspermum **pygmaeum** (King & Prantl.) Holttum, Kew Bull. 14:275. *Sarcochilus pygmaeus* King & Prantl.

PRELIMINARY STUDIES IN THE GENUS STANHOPEA (ORCHIDACEAE)

C. H. DODSON AND G. P. FRYMIRE

ABSTRACT

This preliminary study is an attempt to bring together the knowledge of Taxonomy, Morphology, Phylogeny and Pollination of the species preparatory to a formal revision of the genus. New information, gathered by population study in the natural habitats, appears to be highly significant to the understanding of this complex group.

The distribution of the species is mapped. The phylogenetic relationships of the genus are considered and it is believed that *Stanhopea* is derived from plants similar to members of the genus *Sievekingia*. The development of the advanced and complex species from the simpler species is discussed and the origin of certain unique species such as *S. tricornis* is considered.

Observations of pollination of *S. tricornis* by *Eulaema meriana* and of *S. bucephalus* by *Eulaema bomboides* are discussed and pollination relationships are indicated as the major means of genetic isolation of the two species.

Two highly variable populations were studied in Ecuador. The advanced and variable complexes in *Stanhopea* are very successful both in area of range and density of population. It is felt that this population structure suppresses speciation as a process, though variability is maintained.

Various nomenclatural problems are mentioned and a key to the species is included. A list of the recognized species is given with their synonyms, and a list is appended of poorly known species which cannot as yet be properly placed.

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To say that the genus *Stanhopea* is poorly understood is an understatement. Rather it is in a state of taxonomic chaos. Before we can say that a genus is understood it is expected that an individual plant, taken at random from a population of similar plants, can be fitted into a species concept. That is to say, it should be possible for a trained botanist to determine whether an individual belongs to a known species or is new and unknown. At the present time the only way to deal with most individual plants of this genus is to name them as new species, thus defeating the whole precept of taxonomy. Throughout its range of distribution *Stanhopea* is characterized by populations which are extremely variable. The variability within a single population can be so extreme as to appear as a hybrid swarm in which are represented many kinds of *Stanhopea* hitherto considered as different species.

Because of the plant to plant variability within a single population, a great number of species have been described from single specimens growing in European greenhouses. Often the origin of these plants was not even known. Only the fact that they were different from the other known specimens was taken into consideration and that difference was considered sufficient reason for a new species description. It has been estimated that at least 500 names have been proposed in *Stanhopea* (Ames and Correll, 1953). This estimate is high, actually only slightly over 100 names have been published. Recent works have reduced that number to between 25 and 50 which are considered as even reasonably valid.

One of the problems involved in the classification of this group is that the flowers are large and fleshy and of intricate structure. They do not preserve well as herbarium specimens and many of the structures of the lip in particular are destroyed or altered in drying. The flowers are not long lasting and seldom persist on the plant for more than three or four days. They are therefore difficult to study

in the field since not many flowers can be seen at any one time within a population. Their period of flowering is often extended over a period of from five to seven months and a plant which is not large will generally flower only once in a given year.

Since they are difficult to study in the herbarium it has been suggested that the only way to straighten out the taxonomic confusion in the genus would be by persistent field work. Our work bears out this suggestion and we do not as yet feel qualified to publish a revision of the genus even though we have studied a considerable number of large populations. We have also studied most of the available herbarium material, but find it hopelessly unrewarding. Such large fleshy flowers as are found in this group do not, as a general rule, make good specimens when crushed and dried. Even after boiling, the critical characters are often lost and determination is difficult. Our experience indicates that dried specimens made from the same plants on different occasions are so altered in drying that they can easily be given separate species designations. This situation is particularly true in certain of the critical species groups which are separated on small differences in structure of the fleshy parts of the lip.

Perhaps all is not as hopeless as it appears on the surface. A number of workers have made limited regional studies for orchid floras. A survey of their work reveals that though they do not all agree, they do not seriously disagree in respect to the majority of the species. In fact, some species appear to be remarkably distinct and do not demonstrate significant variation within their populations. Therefore they are given recognition by each of these workers when they occur in regions treated by them.

When the species in which the problems occur are separated from the ones which are distinct we find that the latter group is not a difficult one. Each species has a distinct distribution and to a certain degree a distinct habitat. Within the problem group the species vary tremendously yet they are in many respects remarkably alike, particularly in morphological characteristics. We feel that this is the key to the problem. They are not only remarkably alike, they *are* alike and only represent variations of a pattern If these complexes were treated as representing fewer species each of which may vary considerably within a particular population, then the genus probably could be treated taxonomically and could be understood.

Morphology

Let us consider just what combination of characteristics place a plant in the genus *Stanhopea.* The vegetative characters are surprisingly uniform, so much so that it is nearly impossible to distinguish species without flowers. All are epiphytic or lithophytic. The pseudobulbs are usually large, ovoid, ribbed and unifoliate. The leaves are broad, elliptic-lanceolate, contracted into a petiole at the base and are strongly veined and plicate. The inflorescence consists of a short pendulous raceme with several broad, papery bracts. The flowers are large, long pedicellate and shielded by a papery bract, this often brightly colored and generally similar in aspect to the sepals and petals. Nearly all species produce a strong fragrance, some being agreeable and others not. The sepals are membranaceous and concave, the dorsal sepal is free and erect and the lateral sepals broad, reflexed and connate at

Fig. 1. Distribution of the genus Stanhopea.

the base. The petals in most species are membranaceous, subequal to the dorsal sepal and recurved. The principal characters which separate the species are to be found in the labellum. In general, the lip consists of three parts: the hypochile or globular, concave part nearest the base of the flowers; the mesochile, which is short and often projected on each side to form horns; and the articulated epichile, which is variously shaped but usually ovate. Certain of the species, such as S. *ecornuta* Lehm. and S. *pulla* Rchb. f., simply have a saccate, entire lip which would correspond to the hypocile of the more complex forms. These should perhaps be considered as the more primitive forms and later discussion will attempt to show why. The column is rather similar in most of the species and is elongate and rather slender with or without broad lateral wings. The anther is ventral, incumbent and two-celled. The pollen apparatus consists of a lanceolate viscidium which rests on an elongate spine-like rostellum, a stipe which is long and narrow, and the two pollinia which are elongate, quite thin, and recurved. The stigma forms a pocket under the rostellum.

Distribution

The genus is distributed from central Mexico through Central America and most of northern South America into southern Brazil The plants are generally found in localities where at least some shade is afforded and where they will rarely

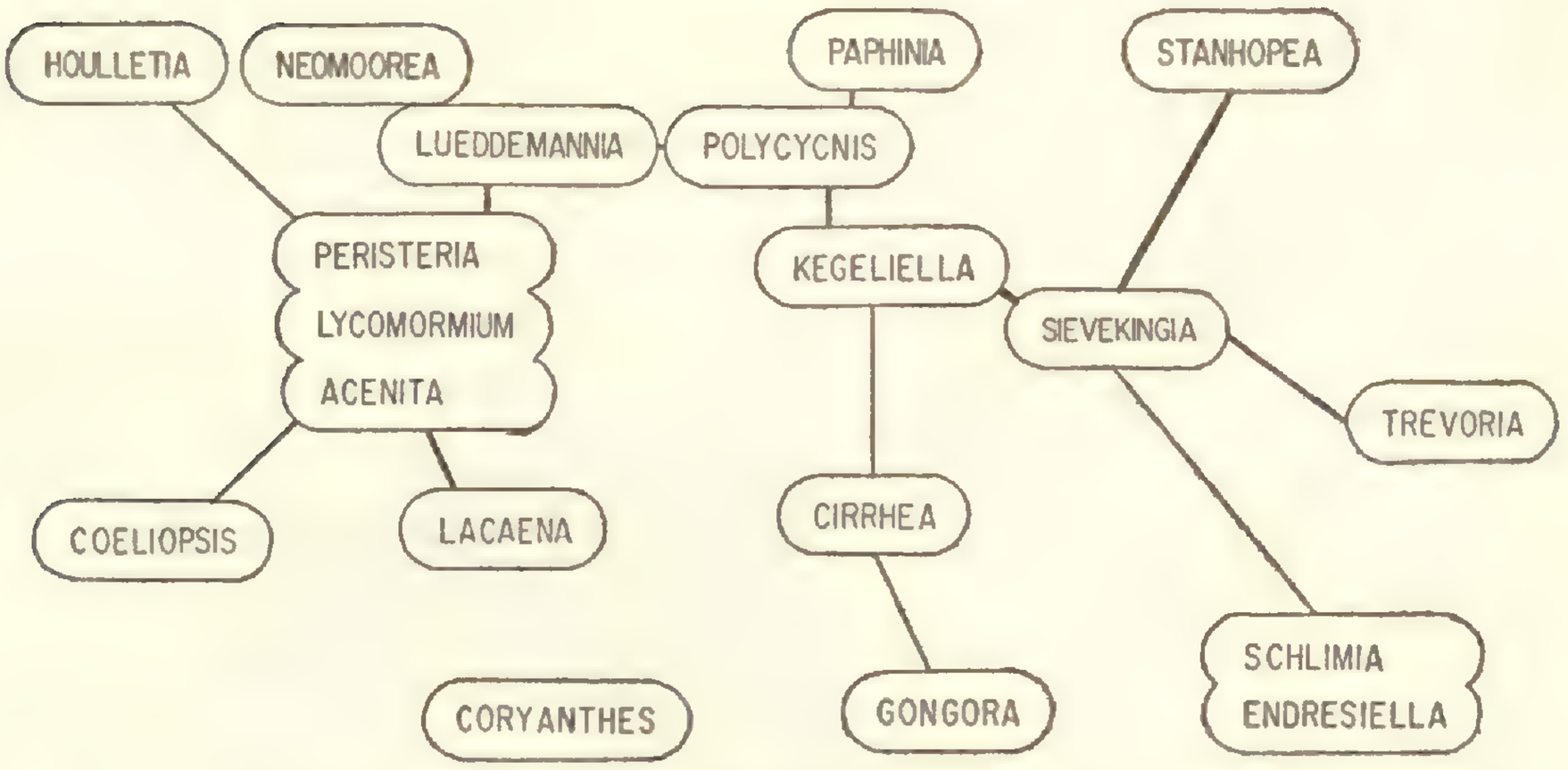

Fig. 2. A diagram of suggested generic relationships within the tribe Stanhopeinae.

become dry. They can withstand prolonged periods of moderate drouth but need considerable water during their growing season.

Figure 1 shows the distribution of the genus. *Stanhopea lewisae* Ames & Correll occurs in Guatemala and Costa Rica. *Stanhopea ecornuta* Lindl. occurs in Honduras, Guatemala, Nicaragua and Costa Rica and S. *cirrhata* Lindl. is found in Nicaragua and Costa Rica. *Stanhopea pulla* Rchb. f. is found in Costa Rica and Panama. *Stanhopea grandiflora* Lindl.* extends from Trinidad through Venezuela, northern Brazil and the Amazon drainage region of Colombia, Ecuador and Peru. *Stanhopea rodigasiana* Hort. and S. *reichenbachiana* Roezl. ex Rchb. f. are little known species which occur in Colombia. *Stanhopea connata* Kl. occurs in eastern Ecuador and Peru and S. *tricornis* Lindl. is restricted to coastal Ecuador and southern Colombia. The remaining species in the genus fall into two major complexes. The first of these groups include S. *insignis* Frost, S. *tigrina* Batem., S. *martiana* Batem. ex Lindl. and S. *saccata* Lindl. The second group is composed of S. *oculata* Lindl., S. *bucephalus* Lindl., S. *wardii*. Lodd. ex Lindl., and a considerable number of lesser known forms which are quite similar. These two groups occur throughout the range of the genus from Mexico to southern Brazil; however, certain forms are restricted to geographic regions.

Phylogeny

The genus *Stanhopea* was taken by Bentham (1881) as the type of the subtribe and thus the name Stanhopeinae should be used in place of Gongorinae Schltr. (See Dressler and Dodson, 1960). As close allies *Stanhopea* has the following genera: *Sievekingia, Polycycnis, Paphinia, Cirrhea* and *Gongora* and perhaps *Peristeria* and *Houlletia.* All of the species within these genera have a labellum which is more

*See the section on Taxonomy for the reason for using this name in place of the commonly used S. *eburnea* Lindl.

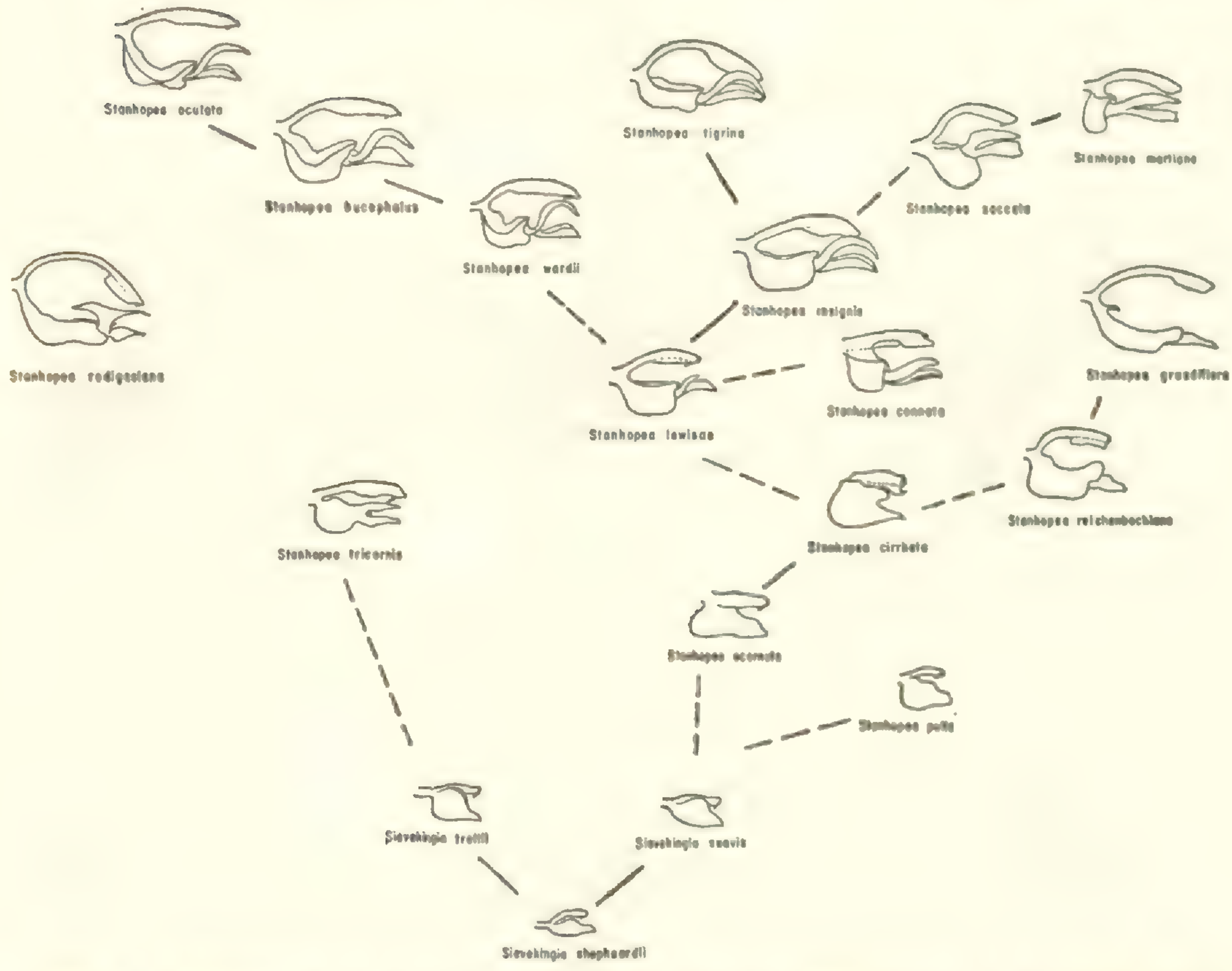

Fig. 3. A diagram of the lip and column of the members of *Stanhopea* and the closely allied species of *Sievekingia* suggesting relationships between the species. Solid lines represent close relationships, while dashed lines represent relationships which are more distant or less clear.

or less divided into a hypochile and an epichile. Figure 2 illustrates a possible phylogenetic series demonstrating the relationships of the genera within the Stanhopeinae.

We do not feel that a discussion of the phylogenetic relationships of the other members of the Stanhopeinae would fall within the purpose of this paper and therefore will only discuss those genera which seem to be directly involved with *Stanhopea* in a stepwise progression from the simple to the complex. The genera placed at the center of the diagram in Figure 2 have a rather simple labellum and as the list radiates outward toward the more advanced genera the lip becomes more complicated.

Figure 3 demonstrates our concepts of the origin and development of the Stanhopeas from the poorly known genus *Sievekingia*, a genus of about seven species. In general the plants are very similar to small immature Stanhopeas and for this reason are often neglected by collectors. Very few specimens of these plants are in herbaria and in several instances the type is the only specimen in existence. Members of this genus were not discovered until late in the 19th Century and thus did not receive so many generic names as some of the earlier discovered members of the subtribe. Without doubt certain of the species placed in *Sievekingia* show fewer morphological relationships to each other than do the following genera to each other: *Acineta*, *Lycomormium*, *Peristeria*, *Coeliopsis*,

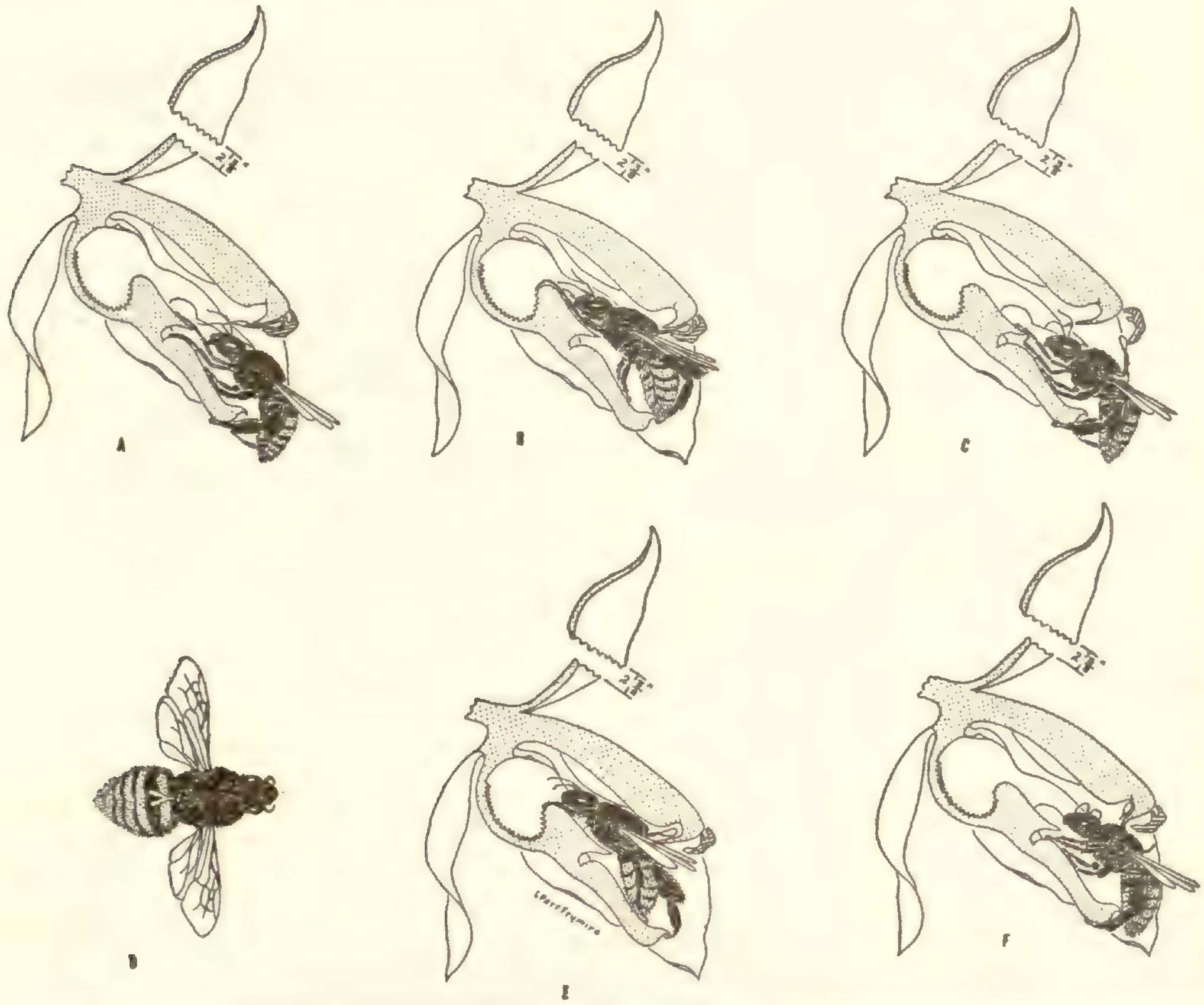

Fig. 4. A diagrammatic representation of the pollination of *Stanhopea tricornis* Lindl. by *Eulaema meriana* A. Bee entering the flower. B. Bee backing out of the flower with the spine of the rostellum engaged under the metathorax. C. Bee leaving the flower with the viscidium attached to the metathorax. D. Bee in flight with the pollinarium in place. E. Bee after entering another flower, showing the pollinia inserted in the stigmatic cleft. F. Bee leaving the 2nd flower, showing the pollinia left in the stigmatic cleft.

Neomoorea, Lacaena and *Lueddemania.* The flowers of the Sievekingias are for the most part less complex than the Stanhopeas. *Sievekingia shepheardii* Rolfe has a semierect inflorescence with rather simple flowers which have only a slightly lobed, truncate lip with a simple fimbriate callus in the center. This is certainly the most primitive known species at least in respect to the labellum. *Sievekingia suavis* Rchb. f. and S. *peruviana* Rolfe have somewhat larger, erect side lobes which form a concave hypochile at the base of the lip. From this point the close relationships of the more primitive Stanhopeas are obvious. It is a simple step from *Sievekingia* to *Stanhopea ecornuta* and S. *pulla* in which the lip is saccate and without the complicated mesochile and epichile of the more advanced Stanhopeas.

Stanhopea cirrhata (Fig. 8) is probably an advancement from a plant similar to S. *ecornuta* (Fig. 6) or S. *pulla* (Fig. 7) through the development of lobes along the upper edge of the hypochile. In other respects S. *cirrhata* is rather similar to the two primitive species except for the narrow, caudate wings formed along each

Fig 5. A diagrammatic representation of the pollination of *Stanhopea bucephalus* Lindl. by *Eulaema bomboides* Friese. A. Bee attempting to land on the waxy surface of the hypochile. B. Bee falling down through the flower.

side of the column. This may be the basic form from which the two major branches of *Stanhopea* have developed. On one side, S. *reichenbachiana* (Fig. 10) could have been derived from S. *cirrhata* and could well have been the form from which *Stanhopea grandiflora* (Fig. 11) developed. *Stanhopea grandiflora* has a fairly complex lip with short horns produced from the hypochile rather than from the mesochile as in many species.

Stanhopea cirrhata could also be considered as similar to the ancestral form from which S. *lewisae* (Fig. 13) developed. *Stanhopea lewisae* has very small, slightly developed horns on the mesochile. Most of the advanced species with well developed horns on the mesochile may well have been derived from S. *lewisae* or a similar form.

Stanhopea tricornis (Fig. 9) shows little relationship to the other species in the genus. The petals are thick and fleshy and are held parallel to the lip and column. The lip has a hypochile which is only slightly saccate, no true mesochile and a very thick and fleshy epichile. The horns are produced as an extension of the hypochile and a sharp spine-like callus forms a third horn between the two lateral horns in the place of a mesochile. Two possibilities can be postulated for the origin of this unique species. First, it could have developed through evolution from the other known species of primitive *Stanhopea* as an isolated form. No intermediates are known, however, between this species and the other known Stanhopeas. The second hypothesis may seem a bit far-fetched, but there is some morphological evidence for derivation of S. *tricornis* from a species of *Sievekingia*, S. *trollii* Mansf., recently encountered as sympatric with this *Stanhopea*. This *Sievekingia* has petals similar to S. *tricornis*. The plant is so similar that it doubtless has been passed over by previous collectors (including ourselves) as a young *Stanhopea*. A colored slide taken of this species, without a scale to indicate size, was at first

determined as a highly floriferous form of S. *tricornis*. The lip of this *Sievekingia* is saccate at the base, has two side lobes which flare outward and an epichile very similar to S. *tricornis*. The callus of the lip is in some respects similar to the center horn of S. *tricornis*. It seems feasible that S. *tricornis* may have been derived by way of this species of *Sievekingia*. *Stanhopea tricornis* may possibly have been derived as a result of hybridization between *Sievekingia trollii* or a similar form and some *Stanhopea* sympatric with it in distribution. *Stanhopea bucephalus*, S. *tricornis* and *Sievekingia trollii* are sympatric along the western slopes of the Andes in Ecuador. If chance pollination of *Stanhopea bucephalus* by the *Sievekingia* should occur the resulting intermediate hybrid might well be visited by a pollinator not utilized by either parental species and thereby be stabilized as a species. When an attempt is made to draw an intermediate between the morphological characteristics of the *Sievekingia* and *Stanhopea bucephalus* the result is surprisingly similar to the labellum of S. *tricornis*.

Stanhopea rodigasiana (Fig. 12) is unique in the genus. The strictly one-flowered inflorescence, ovoid, smooth pseudobulbs, bifid rostellum, round viscidium and unique horns on the lip are characters not found in any other *Stanhopea*. In some respects it suggests a possible relationship to *Paphinia*, but it is certainly close to *Stanhopea*. It is surprising to us that this species was never placed in a monotypic genus. Although it is obviously closely related to *Stanhopea* it is sufficiently different from the other species in the genus to allow any taxonomist with a narrow generic concept to separate it without qualms of conscience. The reason for its not having been so separated is very likely that it was not discovered until after the turn of the century, when more care was being taken in such matters. If it had been discovered 50 years earlier when *Peristeria*, *Acineta*, *Lycomormium*, and other closely allied genera, were being separated, it would surely have been considered as generically distinct. We do not believe that it warrants special distinction nor do we believe that so many genera should be recognized in the *Peristeria* complex. We hope that through more careful study of the entire subtribe Stanhopeinae we will be able to develop a useful revision of its members.

The above mentioned species of *Stanhopea* are for the most part easily recognized, have distinct morphological characters and distributional patterns. They present no serious problems to the taxonomist. The remaining species within the genus form the difficult portion. All of them have a more complex labellum than the species previously discussed. The hypochile is saccate and of various sizes but it follows a similar pattern in all of the species. The mesochile is short and inserted on the apex of the hypochile with two lateral, elongate horns of various sizes. The epichile is articulated to the apex of the mesochile and while it may vary in size and proportions, they are all similar. Two major groups can be separated and while we are not yet prepared to present a formal revision of the genus we feel that some designation is necessary in order to be able to group the excessively large number of species names in such a way that they can be discussed with relative ease. We will use the terms "*oculata* complex" for those plants similar to S. *oculata*, and "*insignis* complex" for the plants allied to S. *insignis*. The "*oculata* complex" will therefore comprise those concepts which have a rather long narrow or rectangular

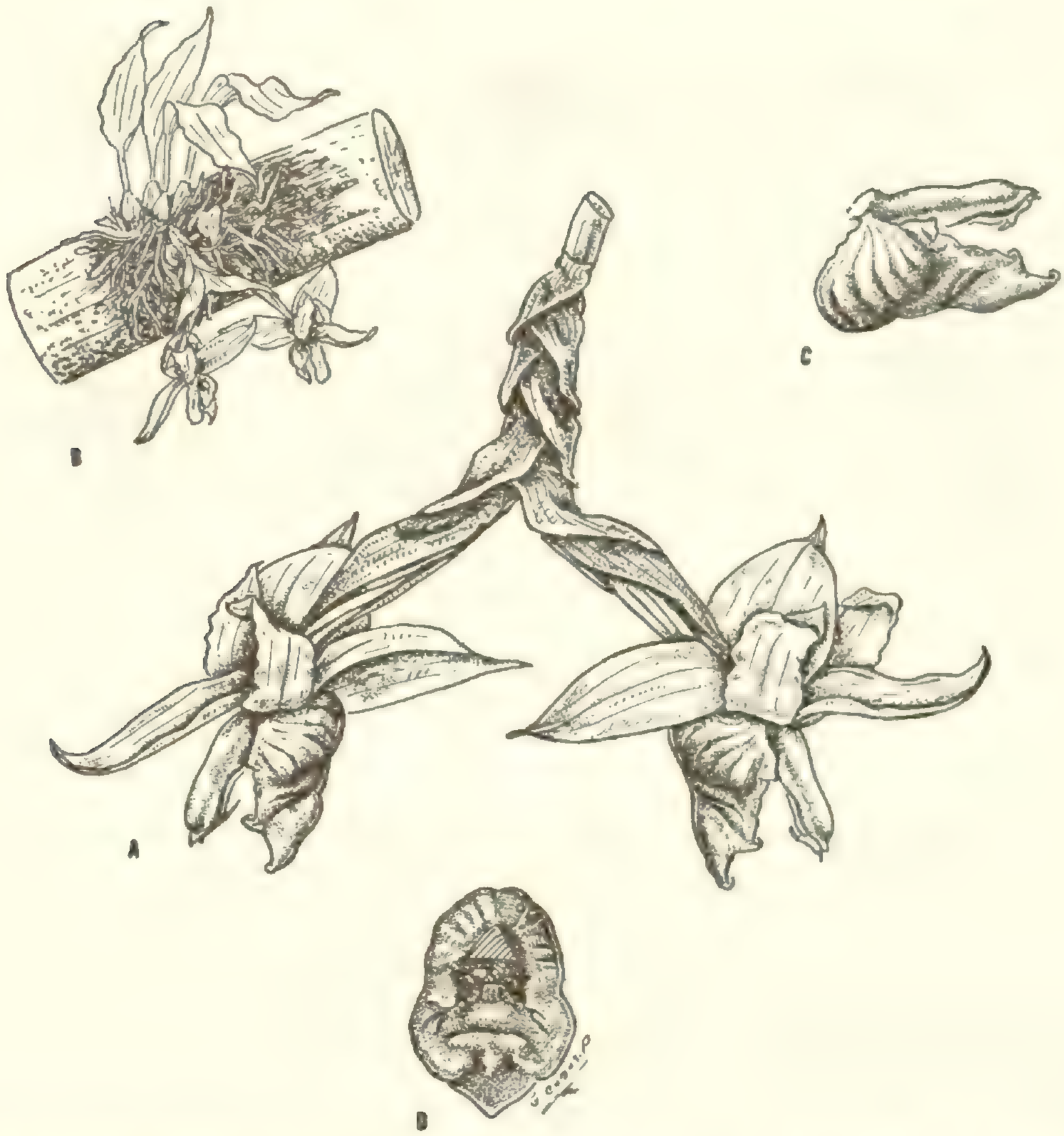

Fig. 6. *Stanhopea ecornuta* Lem. A. Inflorescence (× ⅓). B. Plant habit (× 1/9). C. Side view of the lip and column (× ½). D. Dorsal view of the lip (× 1). E. Pollinarium (× 3).

hypochile, large mesochile horns and always have an entire, acute or apiculate epichile. The "*oculata* complex" comprises such taxa as: *S. wardii* Lodd. ex Lindl., (Fig. 21), *S. oculata* (Lodd.) Lindl. (Fig. 19), *S. bucephalus* Lindl, (Fig. 20), *S. haseloviana* Rchb. f., *S. platyceras* Rchb. f., etc. The "insignis complex" will consist of those forms which have a saccate or globular hypochile, large mesochile horns and either entire, acute or three-lobed epichiles. The "*insignis* complex" comprises such species as *S. tigrina* Batem. ex Lindl. (Fig. 16), *S. martiana* Batem. ex Lindl. (Fig. 17), *S. insignis* Frost (Fig. 15), *S. saccata Batem.* (Fig. 18) and *S. devoniensis* Lindl.

Stanhopea quadricornis Lindl., if such a species exists, has a lip which is within the variation pattern of *S. oculata* with the exception that the base of the thickenings of the margin of the hypochile are projected into short horns. Apparently only one specimen was collected and was named by Lindley. It is quite possible that it was only an aberrant specimen or a hybrid and was not representative of any population.

It seems apparent that *Stanhopea* is a rather terminal group in evolution, with *Coryanthes*, a genus often said to be closely allied to *Stanhopea*, having a derivation

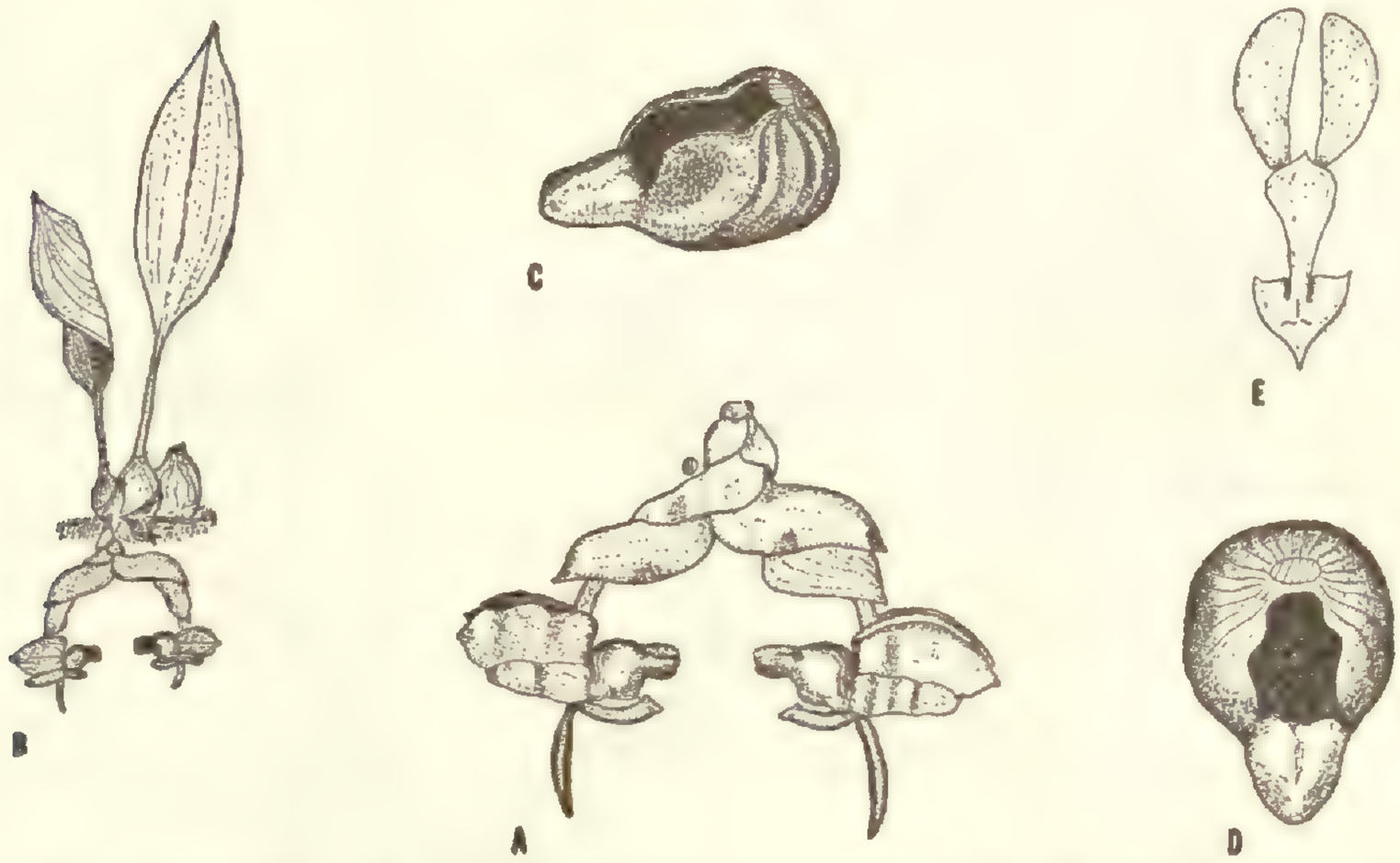

Fig. 7. *Stanhopea pulla* Rchb. f. A. Inflorescence (× 1/3). B. Plant habit (× 1/12). C. Side view of the lip (× 1). D. Dorsal view of the lip (× 1). E. Pollinarium (× 3).

from some similar ancestor, but one probably more closely allied to *Peristeria* than to *Stanhopea*. *Cirrhea* and *Gongora* appear to be the termination of a separate line.

In general, the Orchidaceae appears to be a rather recent but rapidly evolving family in which less extinction is evident than in older families. Such a situation often makes classification difficult due to the intergrading forms, but on the other hand, it makes the tracing of phylogeny easier since closely related groups are still present. We do feel that the Stanhopeas were derived from ancestors very much like some of the species of *Sievekingia* which are known today. The species of *Sievekingia* are not particularly successful, as is evident from their extreme rarity, but may be considered as relict forms locally preserved in relatively hospitable habitats. Such forms would very likely become extinct and be removed from the record if they were members of plant families subjected to more stringent environmental conditions.

Pollination

This paper is perhaps somewhat premature in one respect, that is, the pollinators and pollination mechanisms are not as yet known for all the species. However it may be many years before all the information can be gathered. We feel that the major worth of the paper lies in its discussion of the problems within the genus.

The pollination mechanisms and pollinators of two species have been well worked out and photographed. Pollination studies of the other species will be described when they are known. We have witnessed the pollination of both *Stanhopea tricornis* and S. *bucephalus* in Ecuador.

A future revision of this genus may well be based in large part upon the ideas gained from observations of pollination. Polymorphic genera are often difficult to understand and when confusion is compounded by having highly variable populations, the naming of which has been multiplied on an unrealistic basis, such a genus

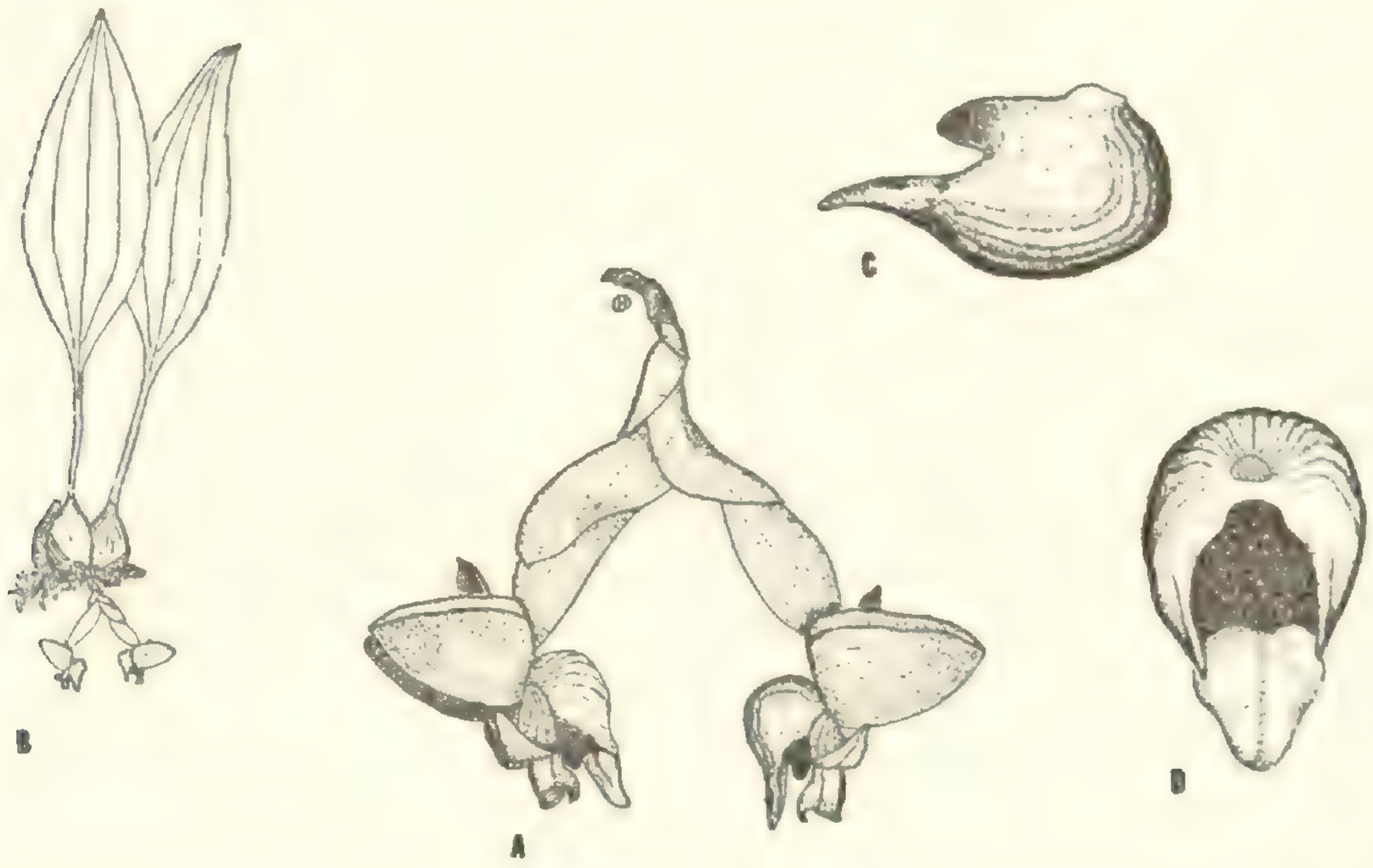

Fig. 8. *Stanhopea cirrhata* Lindl. A. Inflorescence (× ⅓). B. Plant habit (× 1/17). C. Side view of the lip (X ⅔). D. Dorsal view of the lip (× ⅔).

becomes chaotic. Occasionally new techniques or observations from a different standpoint, can provide flashes of insight for the investigator. The totally different pollination mechanisms of these kinds of Stanhopeas, when observed, immediately and clearly made obvious certain of the reasons for the polymorphism within the genus. The first system is typical of most orchids in which the pollinator simply enters the flower after landing on the expanded labellum. The transfer of pollinia occurs as a result of proper positioning of the column and its sexual apparatus in relation to the size and conformity of the particular pollinator. The majority of the species of *Stanhopea* are of this type. These species are not extremely variable and are easily recognized.

The second is a highly complex system in which the flight characteristics of the bee are used in the pollination of the flower. After landing, the bee is clumsy and has difficulty in regaining balance in flight. The bee, unable to grasp the slick surfaces of the pendant labellum, falls through the flower. This characteristic flight habit of the bee probably has contributed to the evolution of an entirely different system of pollination. Though this kind of flower is distinct, it apparently has been unable to preclude occasional hybrids within the related forms but has simply led to more variation. Color and morphology of the unessential flower parts appear to have been subject to little selection pressure for uniformity, and may vary considerably from plant to plant within a given population. The resulting confusion, caused by attempts to name every variant in cultivation, has not only increased out of all proportion but has tended to make the genus nearly impossible taxonomically.

Stanhopea tricornis occurs frequently in old epiphyte covered cacao trees in the region of Quevedo in central, coastal Ecuador. The species generally succeeds best in fairly dense shade and on a large plant the pendant two-flowered racemes are produced throughout the year. Several racemes may be produced by one pseudobulb.

In late January of 1960 we succeeded in finding a plant which had two open flowers (both had been pollinated) and two mature buds which would open the following day. We removed the plant and carefully carried it to our hotel room. Before dawn of the next morning we found the flowers to be open and emitting a heavy perfume very similar to "Diorissimo" manufactured by the Christian Dior Company of Paris, France. We returned to the cacao plantation at dawn and set the plant in a position where it could be easily photographed. At about 9 a.m. a large male bee, *Eulaema meriana* (Oliv.) (tribe Euglossini, family Apidae, *E. dimidiata* is a synonym) came to the flowers, which he proceeded to investigate, apparently searching for the source of the strong fragrance. Meanwhile a second bee of the same species arrived; neither bee seemed familiar with the flower and each searched for some time before discovering the tunnel-like opening, formed by the petals, column and lip, and entering the flower. It might be noted that this is the only species of *Stanhopea* in which the petals are fleshy and held closely appressed to the column. The bee forced upward past the rostellar spine and entered the inner portion of the flower to the hypochile (see Fig. 4). The bee did not attempt to extract food. In backing out the bee encountered the rostellar spine once again. This time the rostellar spine slid under the posterior projection of the metathorax of the bee, and his struggles dislodged the lance-shaped viscidium of the pollinia, which immediately became cemented to the underside of the metathorax. In further backing out he pulled the pollinia from the anther cap. The bee then flew away. Even if the bee had entered the other flower, pollination could not have been accomplished immediately for the stigmatic pocket of *Stanhopea* does not open sufficiently for insertion of pollinia until several hours after the pollinia have been removed. The following morning what appeared to be a different bee but one with pollinia attached to his metathorax visited the flowers. The pollinia became lodged in the stigma and were removed from the back of the bee, thus effecting pollination. In total, five instances of pollination of *Stanhopea tricornis* were observed with six bees, all *E. meriana,* involved.

Other species of *Eulaema* were noted in the immediate vicinity and were quite curious about the camera, approaching to examine it, but showed no interest in the *Stanhopea tricornis* flowers only a foot or so away. These species were *E. tropica* (Linné) and *E. cingulata* (Fab.)* both of which are responsible for pollinating numerous other orchids including several species of *Catasetum, Cycnoches, Sobralia violacea* Lindl., *Maxillaria grandiflora* Lindl., *Aspasia epidendroides* Lindl. and *Pescatoria wallisii* Linden & Rchb. f.

From these observations we can glean the following important points:

1. *Eulaema meriana* appears to be the specific pollinator of *S. tricornis.*
2. *Eulaema tropica* and *E. cingulata* are sympatric but showed no interest in *S. tricornis.*
3. *Eulaema meriana* is attracted to the fragrance emitted by *S. tricornis* and without prior experience with the flower must search to find the entrance.

* These identifications have been recently supplied by Dr. Krombein of the Smithsonian Institution. These two species were previously known as *E. musitans* and *E. fasciata* respectively.

Fig. 9. *Stanhopea tricornis* Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/12). c. Side view of the lip (× ⅓). d. Ventral view of the column (× ½). e. Dorsal view of the lip (× ⅓). F. Pollinarium (× 2).

Flower color and structure are certainly secondary if even of importance in the actual attraction of the bee.

Flowers of S. *tricornis* were carefully examined for nectaries or other anatomical structures which would offer food for the bee. None was found. The fragrance is produced in the hypochile; the other parts, when removed from the flower, have little or no fragrance. The inside of the hypochile is covered with long fleshy hairs which the bee might eat but in the flowers entered by *E. meriana* these hairs did not appear to have been disturbed. It appears then, that the bee is attracted strictly on the basis of fragrance and does not receive food. He apparently does not expect to receive food for he does not lower his tongue, which is so long that it must be lowered and swung forward before a narrow flower is entered. This pattern has been observed in other members of the Catasetinae and Stanhopeinae in which male Eulaemas are attracted by the fragrance and the bees do not appear to receive food of any kind.

In all of these orchids the flowers are generally not long lasting but produce their strong, heady, spicy fragrance in such quantity that they can be detected by

the human nose, a notably weak olfactory organ, at distances of more than thirty feet. The bees are usually quite wary when they first come to the flowers but after being around them for some time seem to become drugged for they fly erratically and can be approached easily. Only the male bees of *Eulaema* appear to be attracted to this type of flower; the females, which are busy with nest building and food gathering to provision the nests, do not approach these flowers. The male bees have never been observed taking part in nest building or care of the nest and seem to leave the nest as soon as possible and live a vagabond life. They secure food from many of the same flowers as the female bees but also visit Stanhopeas, Catasetums, Cycnoches and other flowers which offer only the heady and seemingly intoxicating fragrances. It is possible that the female bees are not attracted to these flowers because they cannot sense them. It is known that female bees of *Apis mellifera,* the domestic bee, have fewer olfactory pits in their antennae than do the males. The only orchids in which both male and female bees were noted were *Sobralia violacea* and *Maxillaria grandiflora. Sobralia* is a rather primitive orchid which does provide nectar for the bee and which is visited by several bees of different families. *Maxillaria grandiflora* provides starchy hairs at the base of the lip. One morphological feature found in the male bees of the Euglossini which is not present in the females is the presence of chemoreceptive hairs on the tarsi of the front legs. The male bees brush these pads through the scratched surface of the labellum of the orchids which they visit.

Stanhopea bucephalus is pollinated in a somewhat different manner. This variable species is distributed along the western slopes of the Andes from elevations of about 400 meters up to 1200 meters and is to be found on the summits of the coastal mountains where they rise to these elevations. It is sympatric with S. *tricornis* in the region of Quevedo and the two species appear to be sympatric for at least 60 kilometers to the south.

Pollination of this species was observed during the month of March at Olimpo on the railroad from Guayaquil to Quito. Unlike S. *tricornis* this species has thin, narrow petals which became retracted and curl up around the dorsal sepal shortly after the flower opens. The horns are not produced as an extension of the hypochile as in S. *tricornis* but are larger and developed from a definite mesochile. Thus there is left a large open space between the lip and the column at the level of the hypochile. The lower part of the column is effectively surrounded, to form a tunnel, by the horns of the mesochile, the epichile and the wings of the column. The pollinator of this species is also a male *Eulaema, E. bomboides* Friese, but this one is only about two thirds as large as *E. meriana. Eulaema bomboides* is a little larger than either *E. cingulata* or *E. tropica.*

Eulaema bomboides is attracted by the fragrance of this *Stanhopea* which is honey-sweet, quite unlike S. *tricornis.* The bees come to the flower of S. *bucephalus* but immediately fly into the space between the column and the hypochile and attempt to land on the hypochile, or they land on the side of the hypochile and attempt to crawl around and enter the hypochile to reach the source of the fragrance. The surfaces of all parts of the lip are waxy and extremely slick, so that the bee can not successfully land and hold fast. He falls down and is guided

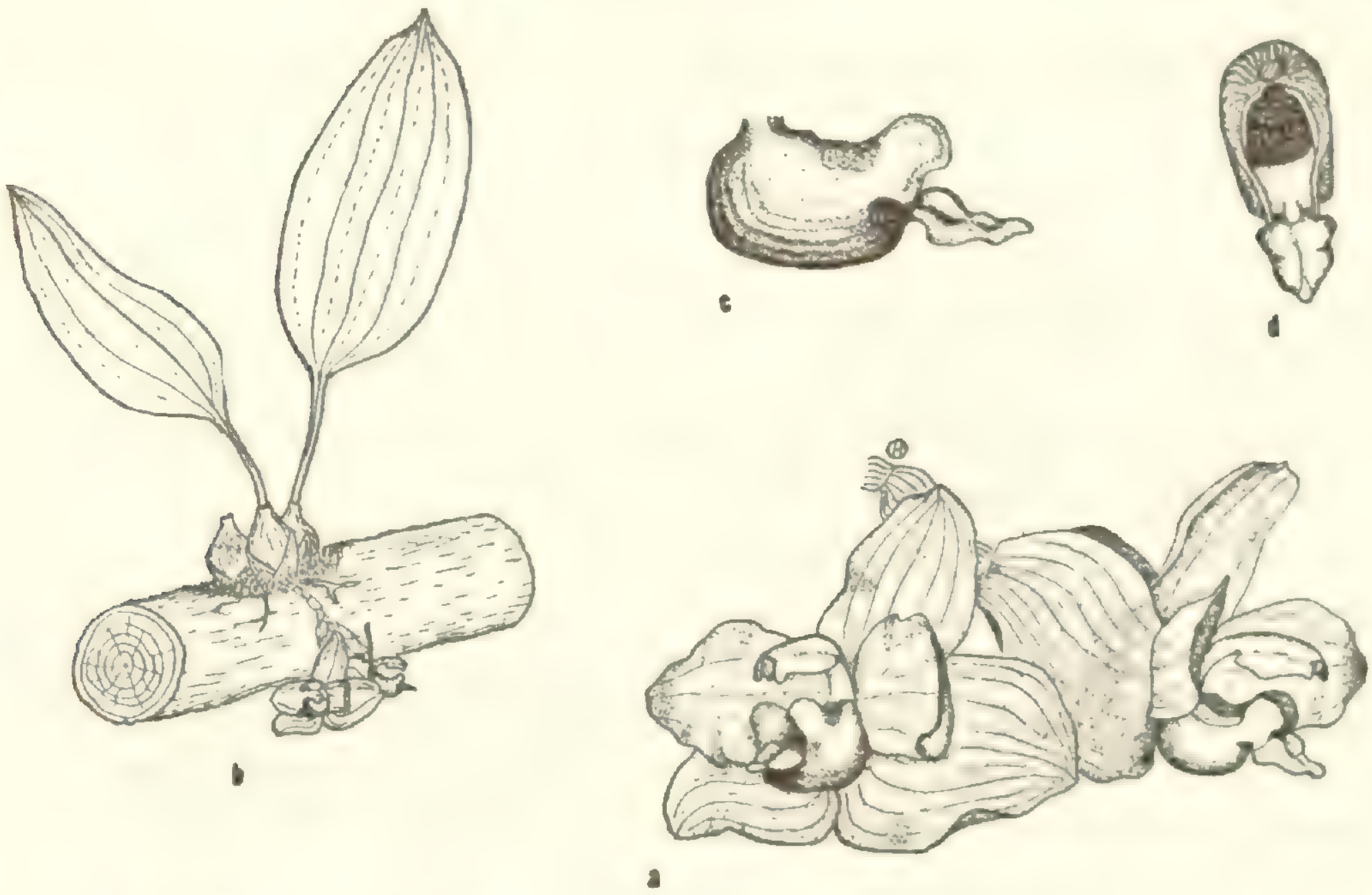

Fig. 10. *Stanhopea reichenbachiana* Roezl. ex Rchb. f. a. Inflorescence (× ⅓). b. Plant habit (× 1/12). c. Side view of lip (× ⅓). d. Dorsal view of the lip (× ⅓).

by the column and its wings at his back, the horns of the mesochile at his sides and the slick epichile beneath him so that he falls directly through the tunnel. At the lower end of the tunnel, almost at its exit, the rostellar spine with the viscidum of the pollinia on its outer surface projects into the path of the falling bee and is caught under the posterior projection of his thorax as in S. *tricornis*. The bee hits the rostellar spine with such force that it gives way and allows the bee to fall through. In doing so the viscidium of the pollinia is cemented firmly into place under the thorax (see Fig. 6). The bee is apparently disturbed and tends to fly away but he repeats the process when he encounters another flower. If the flower is older with an open stigma the pollinia are this time placed in the stigmatic pocket during his fall and pollination is effected.

The pollination of S. *bucephalus* is in many respects quite similar to the pollination of *Gongora maculata* Lindl. as reported by Allen (1956), with the exception that the *Gongora* is pollinated by species of *Euglossa*. *Euglossa* is a genus of bees which is very closely related to *Eulaema* and is also responsible for the pollination of *Coryanthes* (Allen 1950). In *Gongora* the bee, hanging upside down loses its hold on the slick surfaces of the lip, falls and is guided down the pendant column during his fall with the result that he also makes contact with the viscidium of the pollinia much in the same manner as *Eulaema* in S. *bucephalus*.

Several plants of this *Stanhopea* were brought back to the garden of the Instituto Botánico where quantities of *Eulaema tropica* and *E. cingulata* are common and at no time did any of these bees show interest in the flowers. Even when flowering plants of *Catasetum* were placed in the immediate proximity the Eulaemas ignored the *Stanhopea* flowers completely.

From these observations we can add the following facts:

1. *Eulaema bomboides* appears to be the specific pollinator of *S. bucephalus* in the region studied.
2. *Stanhopea bucephalus* is pollinated on an entirely different principle from *S. tricornis.*
3. *Eulaema bomboides* is attracted by the fragrance of *S. bucephalus* which is different from the fragrance of *S. tricornis.*
4. If *E. bomboides* does not visit *S. tricornis* then *S. tricornis* and *S. bucephalus* are effectively isolated genetically.

The last point is by far the most important. *Eulaema meriana* is too large to fall through *S. bucephalus.* If *E. bomboides* is not attracted by the fragrance of *S. tricornis* then the possibilities of the two species of *Stanhopea* forming hybrids are effectively nil. This appeared to be the case. *Stanhopea tricornis* shows very little variability throughout its populations. The sympatric species *S. bucephalus* is quite variable but shows no characters indicating introgression from *S. tricornis.*

If *S. tricornis* evolved in this region with *E. meriana* as its pollinator and *S. bucephalus* was dependent upon a different insect pollinator and a different pollination procedure the two would not hybridize. If by accident a bee of *E. bomboides* did enter *S. tricornis* and effect a hybridization between the two species of *Stanhopea,* and it is feasible that this might occur, then the resulting hybrids would probably find no effective pollinator. If such a pollinator did exist then the chances might be better for development of a completely different, stable species with its own characteristics and its own structurally isolated population.

Interestingly enough, perhaps not all Stanhopeas are pollinated by members of the genus *Eulaema.* The type locality of *Euglossa viridissima* Friese is given as "at *Stanhopea tigrina* at Cordoba and Orizaba in Mexico". If this report is correct, and there is no reason to doubt its validity, it indicates that perhaps some of the species are even more widely separated ecologically than are *S. tricornis* and *S. bucephalus.* Our observations indicate, at least in Ecuador, that Euglossas and Eulaemas are not mutually attracted to the same orchid flowers. Where they are attracted to orchid species of the same genus (i.e., *Eulaema cingulata* is attracted to *Cycnoches lehmanii* and *C. ventricosum* while *Euglossa viridissima* is attracted to *C. egertonianum*) the flowers are extremely distinct morphologically. The principal morphological difference between *S. tigrina* and *S. bucephalus* which would be of importance in pollination procedure lies in the extreme closeness of the column and terminal portions of the lip in the former species whereas in the latter these structures are rather open. A large bee like a *Eulaema* would not be able to fall through *S. tigrina* due to this constriction of parts. On the other hand a *Euglossa* would fall through *S. bucephalus* without touching any of the parts and would be ineffectual in pollination. We feel that the significant factor in this situation does not lie in the morphological form being a deterrent to effective pollination, but rather that the fragrance of the flower does not attract a pollinator which would be ineffective. More likely the morphological structures of the flower have been modified to accommodate the type of pollinator which was attracted to the flower.

Fig. 11. *Stanhopea grandiflora* (Lodd.) Lindl. a. Inflorescence (× ⅓). b. Plant habit (× ⅛). c. Side view of the lip (× ⅓). d. Dorsal view of the column (× ⅓). e. Dorsal view of the lip (× ⅓). f. Pollinarium (× 3).

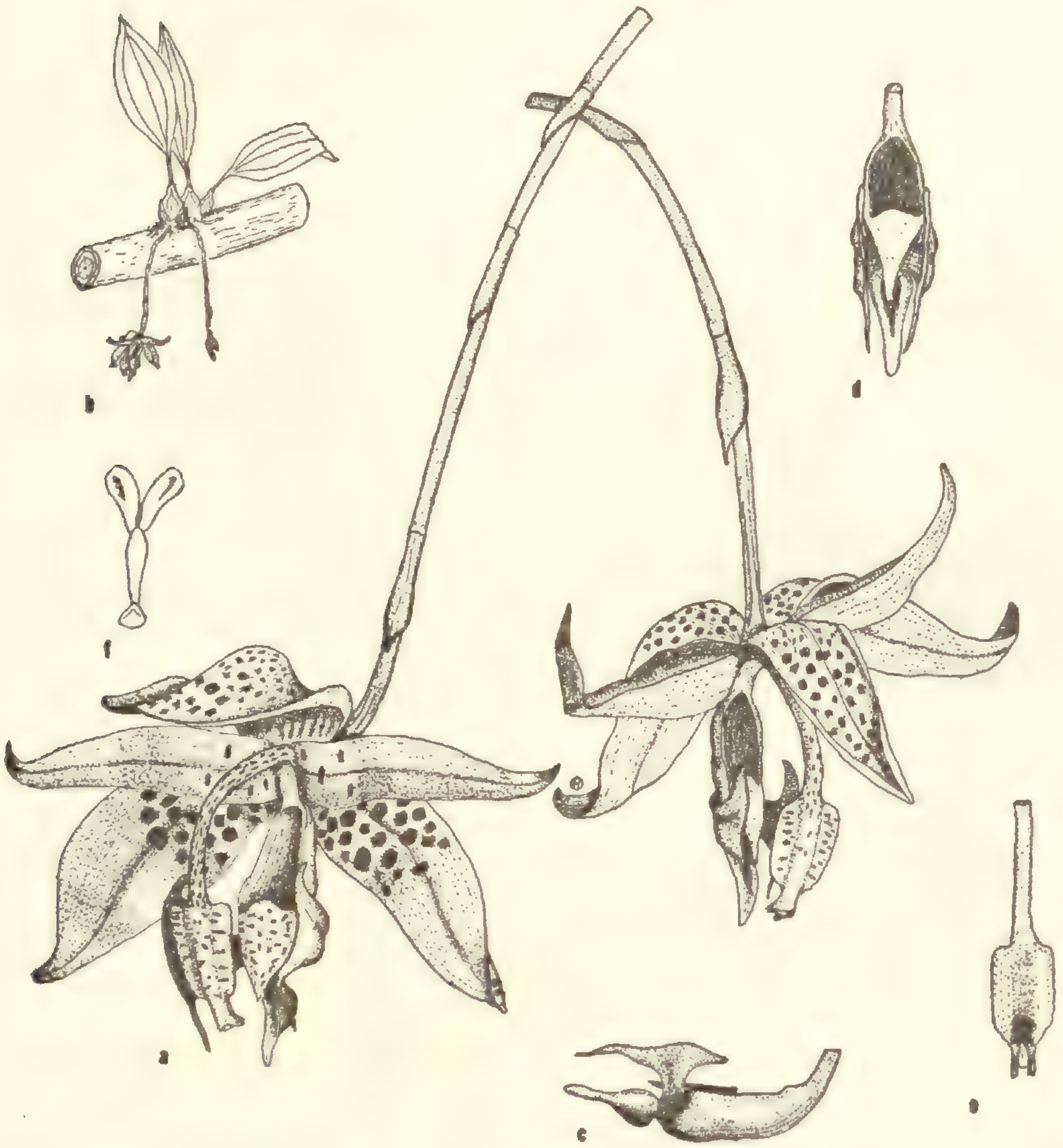

Fig. 12. *Stanhopea rodigasiana* Claes. ex Cogn. a. Inflorescence (× ⅓). b. Plant habit (× 1/15). c. Side view of the lip (× ⅓). d. Dorsal view of the lip (× ⅓). e. Ventral view of the column (× ⅓). f. Pollinarium (× 2).

VARIATION

We have pointed out that populations of species in *Stanhopea* are often extremely variable. Unfortunately no extensive analysis of specific populations are yet available; however, we did superficially study two large populations in Ecuador. The first occurs along the western slopes of the Andes from Macuchi in northwestern Ecuador to Paccha in the south near the Peruvian border. This population is approximately 400 miles long and ranges from 400 to 1,200 meters in elevation.

Near Macuchi some of the plants correspond to a species named by Rolfe as S. *anfracta*. This species is very close to S. *wardii* and had been considered by Lindley as S. *wardii* var. *venusta*. Schweinfurth (1958) has placed it in synonymy with S. *wardii*. Other plants are similar to what has been known as S. *bucephalus*. The population was sampled at four locations through its central portion and was rather uniformly S. *bucephalus* with only occasional plants occurring which could be considered as referable to S. *wardii*. However, at Santa Isabela near the southern extension of the population the situation changed considerably. Plants were so

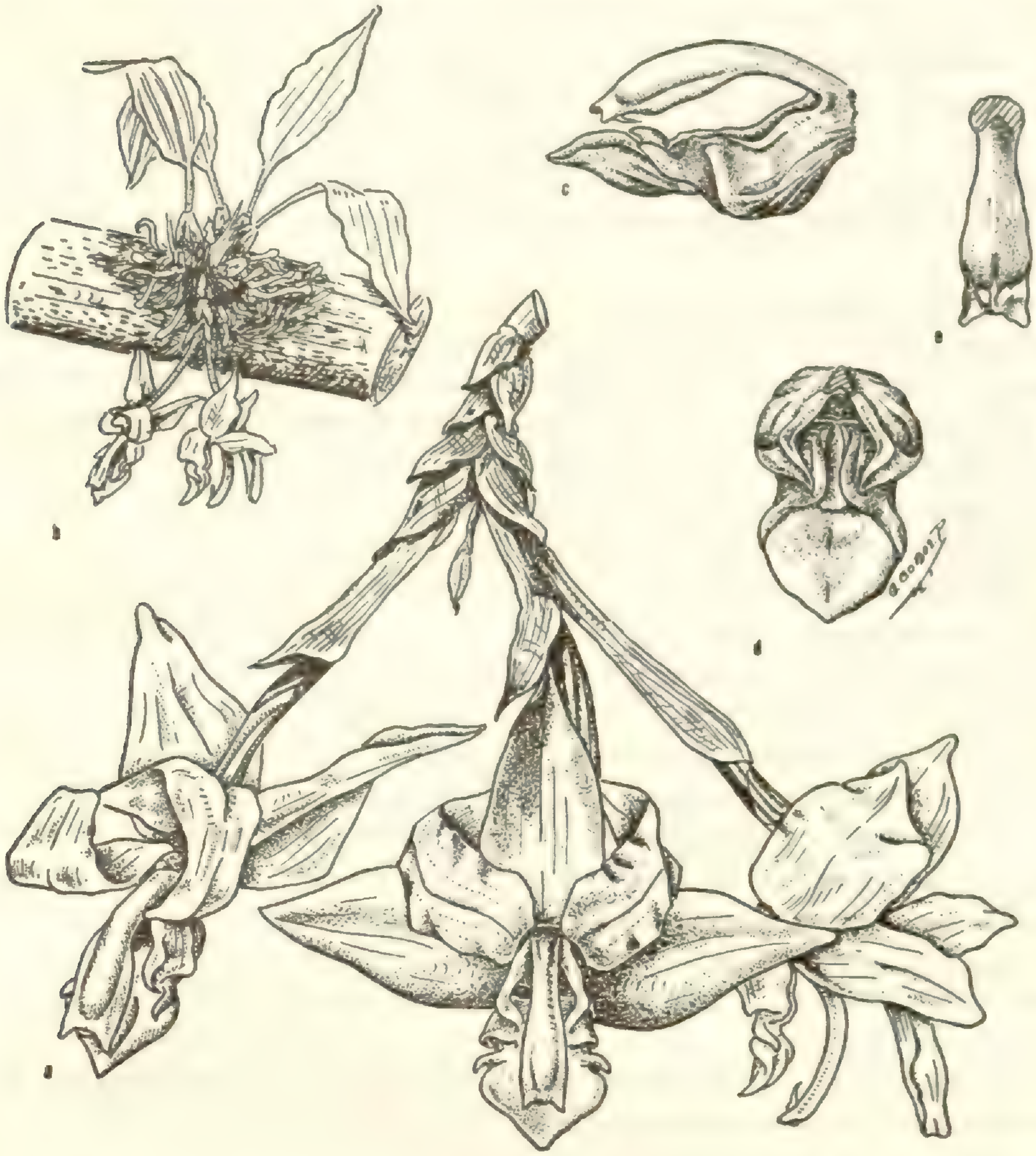

Fig. 13. *Stanhopea lewisae* Ames & Correll. a. Inflorescence (× ½). b. Plant habit (× 1/12). c. Side view of the lip (× ⅔). d. Dorsal view of the lip (× ⅔). e. Ventral view of the column (× ⅔).

variable that specimens were found which corresponded precisely to S. *anfracta*, S. *bucephalus*, S. *graveolens*, S. *oculata*, S. *wardii*, S. *haseloviana*, S. *guttulata*, S. *ornatissima*, S. *platyceras*, and S. *peruviana*. Many plants also occurred in the population which were intermediate between these concepts. Most of these species are actually color forms and many have been relegated to synonymy by other authors. Some of them have been maintained, largely because no botanist knew much about them, for they were described from individual specimens cultivated in Europe and their origins were unknown.

Plants from the population at Paccha, about 20 miles south of Santa Isabela were sent to Europe by a number of early collectors. Kruth named a plant which Humboldt and Bonpland had collected here as *Epidendrum grandiflorum*. Lindley later named another plant from the same locality as S. *bucephalus* and it was illustrated in the Botanical Register, plate 24, in 1845. Reichenbach changed the name to S. *grandiflora*, based on Kunth's name. Another illustration of a plant in the Botanical Magazine, Plate 5278 given as S. *bucephalus* is so inaccurate that four

"species" can be identified from the same plate. Plate 8517 in the Botanical Magazine is actually a plant much nearer S. *wardii*. More recently S. *bucephalus* has been reduced to synonymy under S. *oculata*. This confusion has pointed up the results of describing species from individual specimens without knowledge of the variation within populations. We feel that this situation is not uncommon and clearly demonstrates the need for careful and extensive population studies of the genus.

A second variable population of *Stanhopea* occurs in the valley formed by the headwaters of the Zamora river on the eastern slopes of the Andes in southern Ecuador. The population is extensive and we feel that it demonstrates another of the kinds of phenomena involved in variation of the genus. The upper end of the population reaches a point near Km. 45 on the road from Zamora to Loja, at an elevation of about 1800 meters. The valley is narrow, dense fogs and constant rains are the rule and temperatures are usually low, around 60° F.

Normally the sun breaks through only for an hour or two each day but occasional days are sunny. When the sun is out for several hours the temperature rises to as high as 75° F. The elevation decreases rapidly to the east and at Zamora, 62 km. from Loja, is about 1000 meters. At Zamora the valley levels out and becomes broader, the normal daily temperature is around 75° F. and occasionally reaches 85° F. The weather conditions change little during the year but less rainfall occurs in November and December. The population was studied as far as Yansasa, about 60 km. northeast of Zamora. Here the elevation is near 800 meters and weather conditions are similar to Zamora. In all, the portion of the population studied extended 85 km. and varied from 1 km. in width at the upper end to 3 km. wide at the lower end. Elevations run from 1800 meters at the upper end to 800 meters at the lower end.

Though they are variable in color at the lower end of the population the flowers correspond to *Stanhopea anfracta* Rolfe. The flowers of plants at the upper end are similar to the species described by Schlechter as S. *peruviana* and demonstrate little variation. Both of these species have been reduced to synonymy under S. *wardii*. A cline occurs from the upper end of the population to the lower, the plants in the center having flowers essentially intermediate between the extremes. Variation increases considerably toward the lower end of the population. Vegetatively the plants are indistinguishable throughout the population.

The flowers of the plants at the upper end of the population are morphologically nearly identical to the flowers at the opposite extremes but are colored quite differently and are much thicker in substance. The flowers are completely tangerine-yellow with no other color involved. The sepals and petals have heavy texture and are not reflexed. The flowers usually last for eight days.

At the lower end of the population the flowers are thin in substance and have their sepals and petals strongly reflexed. The basal part of the lip, sepals and petals are yellow-orange flecked and spotted with maroon-red, and the extremities of the sepals, petals and lip are white flecked with red. The flowers last only one or two days. Plants from around Zamora had flowers more or less intermediate between the two extremes in all characters.

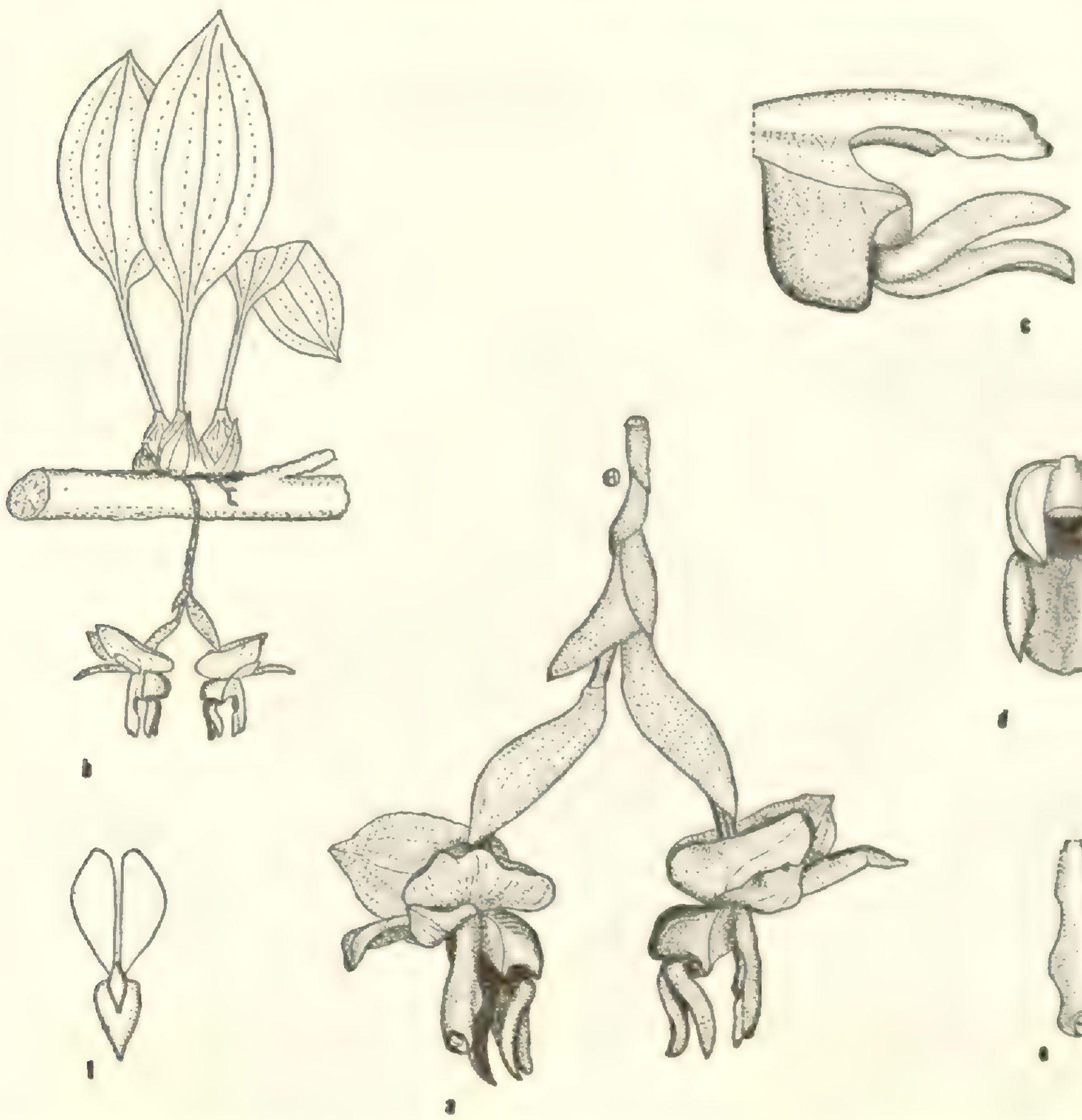

Fig. 14. *Stanhopea connata* Rchb. f. a. Inflorescence (× ⅓). b. Plant habit (× 1/9). c. Side view of the lip (× ⅔). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½). F. Pollinarium (× 2).

From Zamora to Yansasa bees of the genus *Eulaema* were very common. One species in particular was quite common and appeared much like *E. bomboides.* They were of the same size but slightly different in color pattern and probably represent *E. nivofasciata* Friese. Though none was actually observed pollinating Stanhopeas it is probable that they are the pollinators. *Eulaema cingulata* was also common and while they visited other flowers placed in proximity they showed no interest in Stanhopeas and would not enter them.

The bees of this genus are partial to the warmer tropical climates. They nest in hollow limbs or in holes in embankments and their nests have not been encountered at elevations above 1,000 meters in Ecuador. From Zamora to Yansasa they are commonly observed visiting *Costus, Inga* and *Bixa.* They are fast flying bees and are capable of long flights. They are seldom seen in the upper end of the valley and then only on the rare, sunny, warm days. It would appear that they do not nest in the upper extensions of the valley. Plants in the lower regions commonly produce one or two seed capsules indicating considerable visitation by the insects. In the upper regions, on the other hand, seed capsules are rarely encountered.

Fig. 15. *Stanhopea insignis* Frost. a. Inflorescence (× ⅓). b. Plant habit (× 1/12). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½).

This population in some respects appears rather typical of the populations of *Stanhopea* in Ecuador. It is not as complex as the population of *Stanhopea* on the western slope of the Andes which is extremely variable in the direction of *S. wardii* in its northern portion, rather stable in its central portion corresponding to *S. bucephalus* and mixed with typical *S. oculata* in its southern extension. It is our opinion that this type of variation is typical of *S. oculata* and allied species throughout their range. It would appear that the relatively stable, heavy substanced, long lasting type of flower at the upper extension of the Zamora population may be due to strong natural selection for that type of flower. In the upper elevations where pollinators are not abundant it would be of more value to the population to have long lived flowers which would have a greater possibility of visitation and pollination. Such flowers may have to wait several days for weather conditions to be satisfactory for bees to reach them. Short lived flowers would stand little chance of being visited and therefore would rarely reproduce. Long life in these flowers depends on thickness of their parts. A selection pressure is therefore exerted for

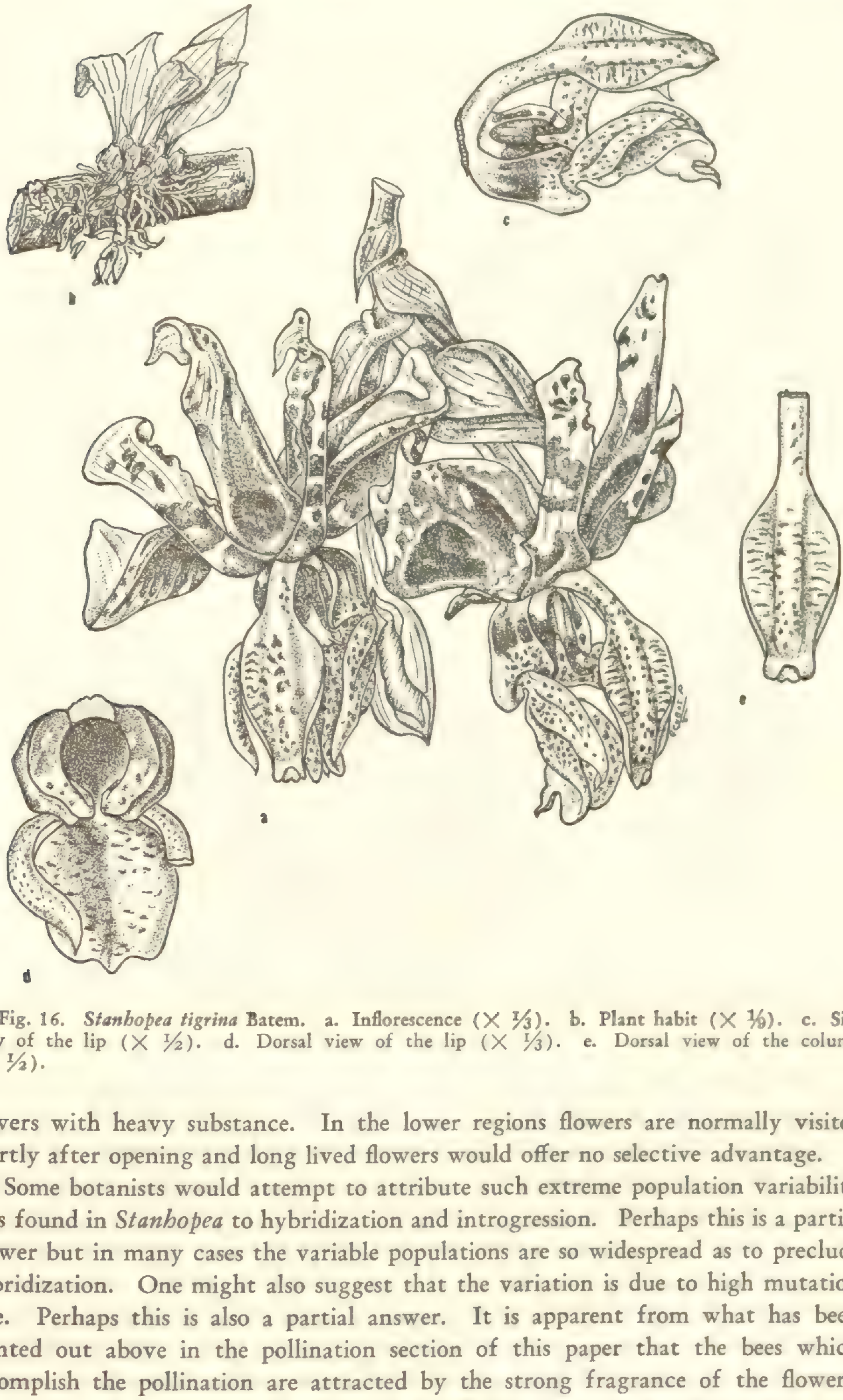

Fig. 16. *Stanhopea tigrina* Batem. a. Inflorescence (× ⅓). b. Plant habit (× 1/9). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ⅓). e. Dorsal view of the column (× ½).

flowers with heavy substance. In the lower regions flowers are normally visited shortly after opening and long lived flowers would offer no selective advantage.

Some botanists would attempt to attribute such extreme population variability as is found in *Stanhopea* to hybridization and introgression. Perhaps this is a partial answer but in many cases the variable populations are so widespread as to preclude hybridization. One might also suggest that the variation is due to high mutation rate. Perhaps this is also a partial answer. It is apparent from what has been pointed out above in the pollination section of this paper that the bees which accomplish the pollination are attracted by the strong fragrance of the flowers. The color, and to a degree, the form of the flower appears to be of minor importance in its pollination. This is also true in the genera related to *Stanhopea*, such as *Gongora* and *Coryanthes*.

Fig. 17. *Stanhopea martiana* Batem. ex Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/9). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½).

If the attraction of the fragrance is so strong, color may be a minor factor in selection and the bees will still visit the flowers even if color varies widely. Also form could vary widely in parts which are not essential to the actual mechanisms of pollination, allowing variants due to mutation to remain within the population as fully effective breeding members contributing to the gene pool as a whole. In S. *oculata* and its allied species the characters which vary the most are the form of the hypochile of the lip and the color of the lip, sepals and petals. These are characters which are not actually involved in the mechanisms of pollination, and may not be important in the actual attraction of the pollinator. Selection would not be strong for these characters and a plant which deviated from the norm to a considerable extent could still remain a breeding member of the population as long as it retained the character of fragrance to attract the pollinator and the correct propor-

Fig. 18. *Stanhopea saccata* Batem. a. Inflorescence (× ⅓). b. Plant habit (× 1/5). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½).

tions of the tunnel of the lip, formed by the mesochile and column, to properly place the pollinia for transport by the bee to another flower.

The fact that cross-pollination is nearly obligate in these genera may be of importance also. Certainly more variation would be produced, maintained and dispersed in a population of obligate cross-pollinating plants than in a population where self-pollination is possible and often of regular occurrence. Certain of the genera in the Catasetinae, i.e., *Catasetum* and *Cycnoches*, are characterized by unisexual flowers which make cross-pollination obligate. These are genera in which the species are notoriously variable. In many of the other genera self-

incompatibility is the rule. Not a great deal of information is available on this phenomenon but the authors have made numerous attempts to self-pollinate *Stanhopea bucephalus* and *Gongora maculata* with no success. The resulting seed pods dropped after a few weeks.

In most of these variable genera the flowers are highly fragrant but extremely short lived, seldom lasting more than two or three days. The fragrance ceases very soon after the flower has been pollinated. It would appear that there is a correlation involved between the characteristics of powerful fragrance and short lived flowers. These species seem to depend on their fragrance to attract pollinators and are usually very successful, for a considerable portion of the flowers are pollinated. They have developed in the direction of stronger and more attractive fragrances but offer no food or nectar to the pollinator. Selection may even favor short-lived flowers which do not attract bees long after their pollination (i.e., do not compete with the younger flowers). Here there seems to be a strong selection pressure for fragrance for pollinator attraction with lower selection pressure for constancy of morphological characters.

Many of the orchids which have long lasting flowers are either not fragrant or are weakly fragrant. These orchids seem to depend on numbers of flowers few of which are ever pollinated. These species for the most part are not as variable as the fragrant types and have developed other mechanisms for attraction of the pollinator. Where populations of these species are extremely variable, it is usually in a relatively limited geographical area and their variability can often be attributed to introgressive hybridization.

Successfulness of the Genus

The objective measurement of success in a group of plants is difficult, as too many factors are involved. Obviously, so called weedy species would rate high on the scale. However, to attempt to rate other plants as being highly successful or only fairly successful is scarcely possible. We do feel, however, that we can subjectively rate the success of a group of orchids in relation to other orchids. In such a subjective sense we can use extent of distribution and density of populations as measuring tools. Many orchids are highly successful in respect to density of population but are limited in distribution. Others have wide distributions but are seldom encountered in quantity in a given area. The majority of the species of *Stanhopea* are in one or the other of these categories. The "*insignis* and *oculata* complexes" on this basis are highly successful in that they are commonly found in quantity (in undisturbed habitats) and have broad ranges. They are to be encountered in any region of the American tropics which provides the basic needs of the plants. They are found from sea level to 7000 feet and grow as well in either location provided there exists sufficient humidity and shade and the temperatures are not too low.

This very success, we feel, contributes to their variability, but on the other hand, may have suppressed speciation. The extremes of the range may be expected to produce forms which are unlike due simply to spatial relations. However isolation is difficult to achieve in a dense and essentially continuous population. In

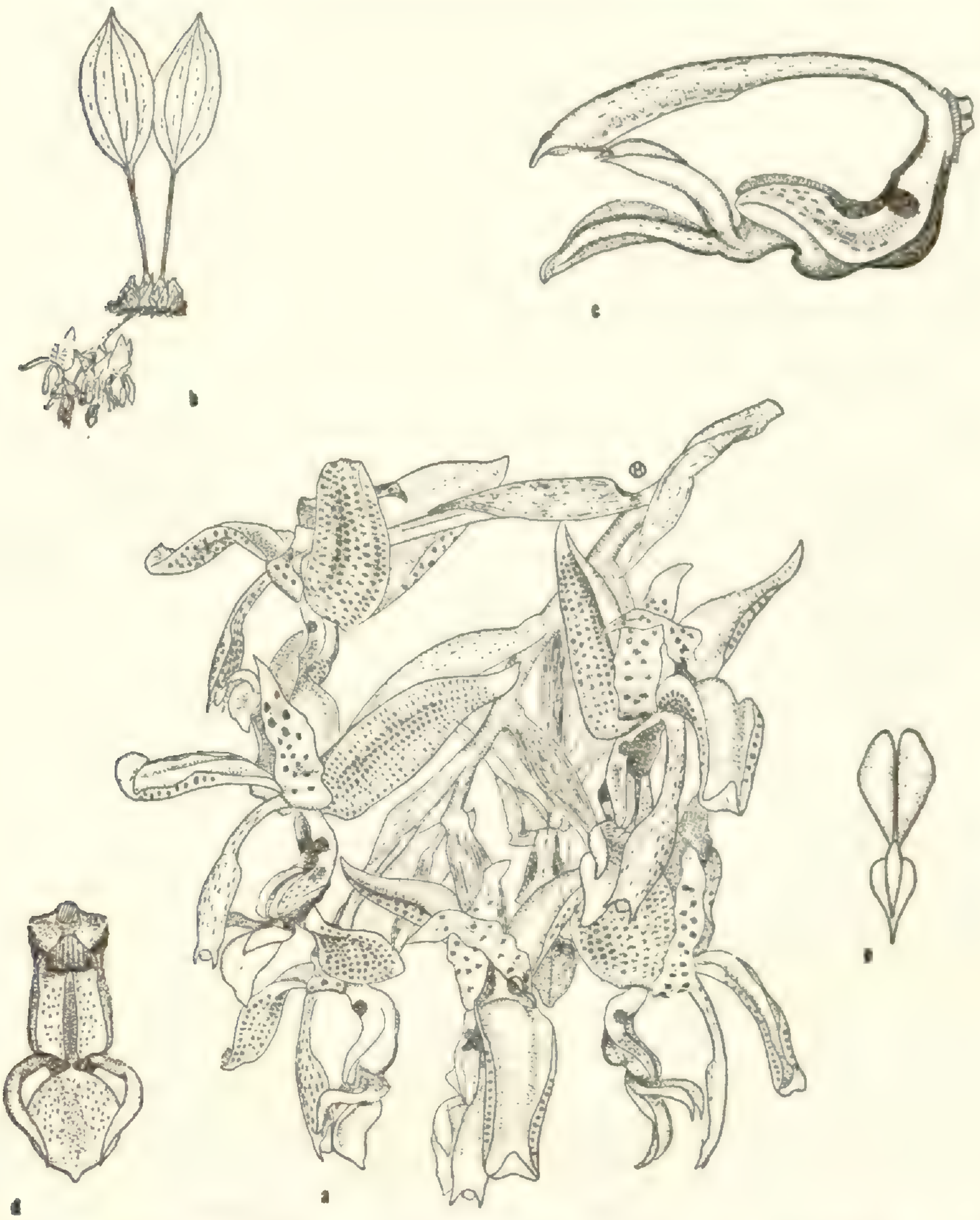

Fig. 19. *Stanhopea oculata* (Lodd.) Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/15). c. Side view of the lip (× ⅔). d. Dorsal view of the lip (× ½). e. Pollinarium (× 2).

this respect "success" and taxonomic diversity may be mutually incompatible.

This situation is by no means limited to *Stanhopea*. The hooded types of *Catasetum* reflect the same phenomena, though not quite to the same degree. In Mexico and middle Central America a form known as *C. integerrimum* Hook. is common and variable. Further south in Costa Rica and Panama intergrading populations known as *C. viridiflavum* Hook., *C. oerstedii* Rchb. f. and *C. maculatum* Kunth occur. From Panama extending through Venezuela, the Guianas and northern Brazil the form known as *C. macrocarpum* L. C. Rich. is found. In Ecuador *C. macroglossum* Rchb. f. is common. All of these populations are highly variable and in Ecuador alone, specimens corresponding to all of these "species" may be found. There is little reason to recognize these species when they are now known to be only representatives of one widely distributed and highly successful popula-

tion. Here, as in *Stanhopea*, speciation seems to be inhibited by the otherwise highly successful population structure.

Gongora maculata Lindl. demonstrates a close parallel. Several species of *Cycnoches, Mormodes, Coryanthes, Epidendrum* and *Oncidium* have similar patterns. Many other instances of highly successful, widely distributed orchids can be given in which the most striking chracteristic is their extreme variability. We feel that speciation has taken a back seat to success in the sense that development of distinct taxa is inhibited where gene flow is unrestricted and selection is weak.

Taxonomy

Perhaps the most successful method of handling the great variability in *Stanhopea* will be to follow that used by Allen (1952) in his particularly workable and useful revision of *Cycnoches*. *Cycnoches* reflects the same kinds of problems encountered in *Stanhopea* and by placing several closely related, intergrading populations, which had been previously known as species, as subspecies under one inclusive species, Allen was able to indicate the close relationships of these populations. In our opinion this is the most practicable manner to handle the problems of such extreme variability in obviously closely related populations. Certainly, it is folly to attempt to apply species or even subspecies names to all of the variants found; the number would be endless. There may be some difference of opinion as to how many subspecies should be recognized, some authors suggesting more and others less. When numerous well authenticated population studies are accomplished in *Stanhopea* it is quite possible that certain of the dubious species within the "*insignis* and *oculata* complexes" will be found to exist as discrete populations and will be sufficiently distinct to be recognized, others will probably be reduced.

Recent correspondence with a rather well informed amateur orchid enthusiast indicates that he has encountered a stable population of a *Stanhopea*. Specimens which he has kindly forwarded appear near the type form of *S. oculata*. He maintains that these are different from typical *S. oculata*, are stable within what he knows of the population and should therefore be recognized as a new species. Perhaps with exhaustive study this population might be found to be distinct throughout its extent and should therefore be considered as a valid species. Our experience with populations of *Stanhopea* in Mexico, Guatemala, Costa Rica, Panama, Ecuador and Peru would indicate that this population, throughout its entire range, would very doubtfully represent even a valid subspecies of *S. oculata*. This case, however, is quite representative of the problems which *Stanhopea* offers and indicates the necessity of thorough knowledge of large percentages of over-all populations before rash action is taken in applying more epithets in the group.

The nomenclature of *Stanhopea* is badly confused and the efforts made by modern workers to clarify the situation have not always been particularly successful. Many of the early descriptions of the species were not accompanied by illustrations and were at best brief. Several of them are nearly impossible to identify with any particular population. One of the unfortunate pitfalls the modern taxonomist encounters is the tendency to make one of these early descriptions fit his concept of a given species or vice versa. Normally the taxonomist has the type specimen

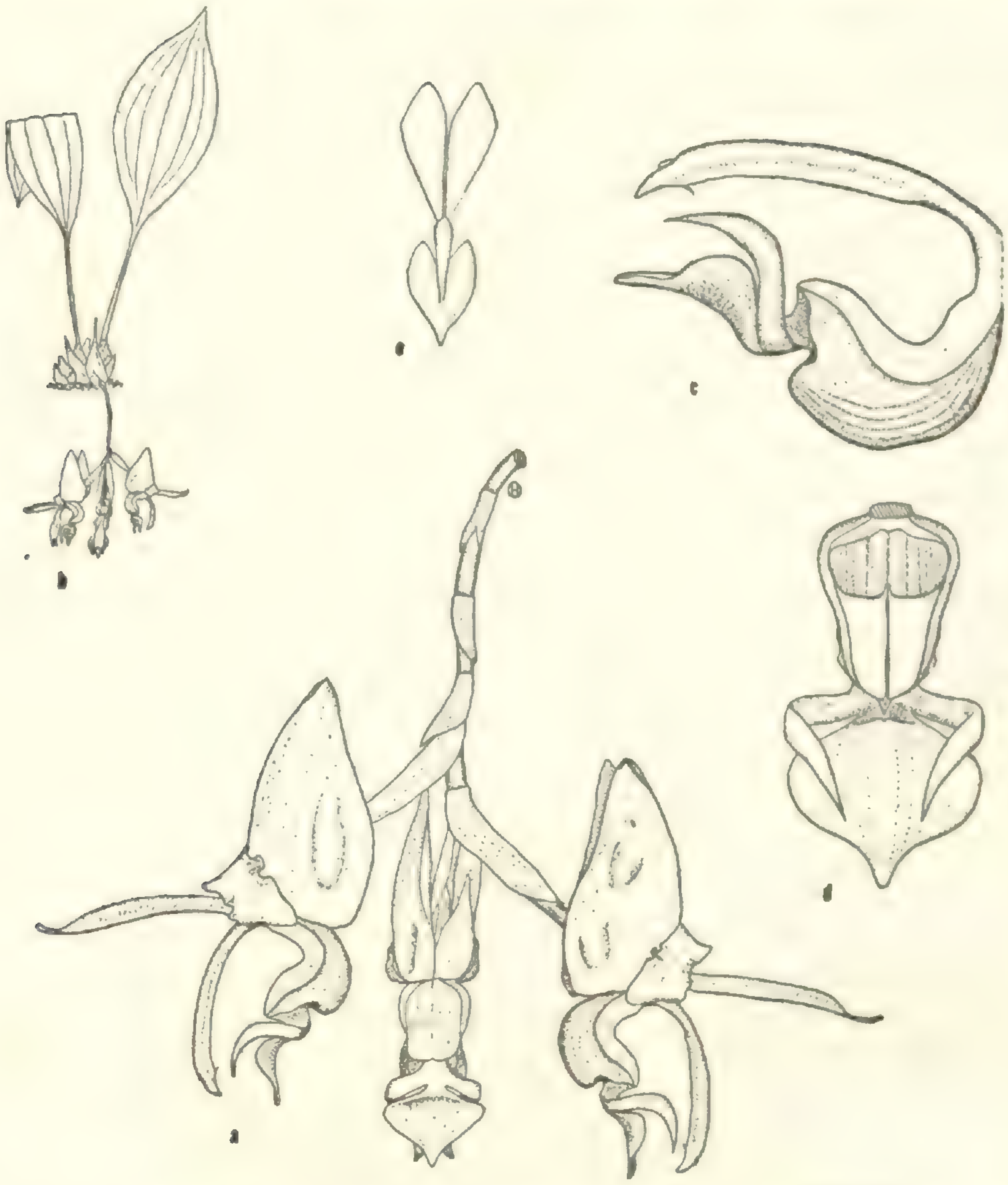

Fig. 20. *Stanhopea bucephalus* Lindl. a. Inflorescence (× 1/3). b. Plant habit (× 1/15). c. Side view of the lip (× 2/3). d. Dorsal view of the lip (× 2/3). e. Pollinarium (× 2).

to fall back on and this specimen, when carefully examined, supplies the necessary information to avoid error. Unfortunately, herbarium specimens of Stanhopeas do not always fulfill this function even when they exist. The critical characters which separate species in this genus are for the most part destroyed in the preparation of specimens.

Many times the type specimen does not reflect the actual structure of the population. An example is to be found in *S. wardii* in which the type description mentions two teeth produced at the base of the hypochile by the extension of the falcate lateral margins. This character is common in the specimens from southern Central America and perhaps to a lesser extent in Guatemala, but actually does not occur in many of the specimens from Mexico, Nicaragua and northern South America, which are certainly referable to this species on every other criterion. To further complicate the situation, this character does occur occasionally in other species such as *S. oculata* and *S. bucephalus*. Doubtless, the type specimen of *S. wardii* did have this character, but the presence or absence of this one character,

since it is not diagnostic of the total population and is found in other species, should not be considered as a criterion for determination. Several other characters help to make this species distinct from S. *oculata* and S. *bucephalus*. Allen (1949) has suggested that Lindley was in error in his description of S. *oculata* and S. *bucephalus*. Allen placed S. *bucephalus* in synonymy under S. *oculata* and re-erected S. *graveolens* which had been considered as synonymous with S. *bucephalus*. We cannot, however, agree with Allen and feel that the epithet, S. *bucephalus*, should be used in place of S. *graveolens*. Since Lindley's descriptions are extremely brief and the later illustrations which he used of his species correspond rather well with his descriptions and with actual populations, we feel that Allen has allowed his splendid knowledge of the Central American species to overshadow the variation of these species in other areas. Since the type specimens yield little information it will always be difficult to resolve this situation.

Another of the confusing situations involved in the taxonomy of *Stanhopea* is the use of the name "*grandiflora*". This name was first used by Kunth when he described and illustrated *Epidendrum grandiflorum* in 1808. In 1828 Loddiges described another plant and named it *Ceratochilus grandiflorus* but the name *Ceratochilus* had previously been used by Blume for an East Indian orchid. In 1832 Lindley transferred the Loddiges plant to the genus *Stanhopea* of Frost and described a similar species as *Stanhopea eburnea*. Later these two plants were found to be conspecific but have been known as S. *eburnea* to the present time. Lindley's name, S. *grandiflora*, is valid and must be used in place of S. *eburnea*. In 1832 Lindley also named a plant which was essentially identical to Kunth's plant as *Stanhopea bucephalus*. The type specimen was a Ruíz and Pavón collection which, as Rolfe (1912) has pointed out, is marked as being from Mexico. It appears that many of Ruíz and Pavón's specimens were mixed with the Sessé and Mociño Mexican collections and a great deal of confusion has been caused by this situation. The probable origin of the Ruíz and Pavón specimen was Peru, as it was then called, or what is now Ecuador. It must have come from very near the same locality as Kunth's specimen since the trails of access to the Andes were very few during this period.

Reichenbach apparently attempted to clear up the situation by transferring Kunth's plant to *Stanhopea* and reducing Lindley's S. *bucephalus* to synonymy under S. *grandiflora* Rchb. f. Unfortunately, Reichenbach's S. *grandiflora* is invalid because Lindley's combination precedes it.

Another attempt to clarify the situation in the "*insignis* complex" has been the reduction of the name S. *tigrina* Batem. to synonymy under S. *devoniensis* Lindl. by Williams (1951). However, the concept, early descriptions, and illustrations of S. *devoniensis* and S. *tigrina* appear to us to be clearly distinct. The plate of S. *devoniensis* in Lindley's *Sertum Orchidacearum* has little resemblance to Bateman's plate of S. *tigrina* in his *Orchids of Mexico and Guatemala* and very likely represents either a rarely encountered species or a hybrid form between S. *saccata* and S. *tigrina*. The figure very definitely resembles S. *saccata* in the features of the lip more closely than it does S. *tigrina*. Williams may have been misled by the color, and was certainly handicapped by the lack of good type material. Occasionally

Fig. 21. *Stanhopea wardii* Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/9). c. Side veiw of the lip (× ½). d. Dorsal view of the lip (× ½).

plants with flowers somewhat like the description and plate (discounting the three-lobed epichile which is lacking in the plate but mentioned in the description) turn up, but are quite rare in comparison to the number of typical *S. tigrina* found in the Mexican populations.

Conclusions

This paper has been written as a discussion of *Stanhopea* preliminary to a formal revision of the genus. Our original intention was to include the revision of *Stanhopea* with this paper but after examination of herbarium material proved to be disappointing we have concluded that only with further field study of living populations can we accomplish a truly meaningful treatment of the genus. We have also found that to merely revise *Stanhopea* and leave the other members of the subtribe Stanhopeinae in the condition which they are at the present time would be to do a less than meaningful work. The members of the Stanhopeinae are so closely intermeshed with *Stanhopea* that revision of the whole group is mandatory. We hope that in the not too distant future such a revision can be accomplished using classical methods of taxonomy combined with modern biosystematic procedures.

In reality then, this paper can only point up the problems involved in the group; it brings up to date the information that is available from the literature and adds our own limited observations of the natural phenomena occurring in the group. These field observations have pointed out the path, so to speak, that should be followed in the study of such a complex and difficult genus as *Stanhopea*. It may well be true that similar procedures will need to be used in treating other problem groups in the Orchidaceae. Our experience indicates that future studies of the difficult subtribe Catasetinae can only be approached through field study. Probably parts of the Sobraliinae, Epidendrinae and Pleurothallidinae will prove to be similar.

Appendix

Key to Stanhopea

a. Lip simple, composed of a saccate hypochile with thickened midlobe forming a non-articulated epichile, mesochile absent; column thick, wingless or narrowly winged with the apex of the wings caudate and extended beyond the anther.

b. Hypochile entire, not projected into side lobes on its upper edges; column wingless.

c. Callus in center of the lip tongue-like, apex of the lip slightly thickened; lip 3.8–4.5 cm. long.....1. S. ecornuta

cc. Callus in center of the lip absent, apex of the lip thick and fleshy; lip 1.8–2.5 cm. long.....2. S. pulla

bb. Hypochile projected into fleshy lobes on its upper edges; column narrowly winged with the apex of the wings caudate and extended beyond the anther.....3. S. cirrhata

aa. Lip complex, composed of 2 or 3 distinct parts, epichile articulated to the hypochile or to a fleshy mesochile that is provided with lateral horns; column slender and arcuate with narrow or broad wings which are not caudate at their apex and extended beyond the anther.

b. Petals erect and fleshy, paralleling the lip and column; mesochile of the lip consisting of 3 horns, one large lanceolate horn on each side and a third horn produced from the center of a fleshy plate between and extending over the epichile.....4. S. tricornis

bb. Petals thin in substance and reflexed; mesochile of the lip with 2 horns on its margins or none.

c. Hypochile of the lip provided with 2 distinct horns or protuberences, mesochile relatively simple and without lateral horns.
d. Hypochile subsaccate provided with fleshy lobes on each side of the apex; column narrowly winged.....5. S. REICHENBACHIANA
dd. Hypochile relatively slender, horns at base slender and recurved, lobes at the apex not fleshy; column broadly winged.....6. S. GRANDIFLORA
cc. Hypochile of the lip with the lateral margins thickened, not provided with horns or protuberences, mesochile with 2 distinct horns.
d. Horns of the mesochile divided at their midpoint to produce a falcate, retrorse appendage as well as a slender forward projecting spine; flowers always solitary. .....7. S. RODIGASIANA
dd. Horns of the mesochile acicular or flat, not divided; flowers normally 2 or more.
e. Horns of the mesochile very short, free for less than 1 centimeter.....8. S. LEWISAE
ee. Horns of the mesochile long, free for more than 2 centimeters.
f. Mesochile obsolete, very short, hypochile conspicuously adnate to the column. .....9. S. CONNATA
ff. Mesochile conspicuous, well developed, hypochile not adnate to the column.
g. Hypochile globose or saccate.....10. *insignis* complex
gg. Hypochile more or less elongate or quadrate.....11. *oculata* complex

List of Species*

1. Stanhopea ecornuta Lem. in Fl. des Serres 2: *t. 181*. 1846. (Fig. 6).
Stanhopea calceolus Hort. ex Rchb. f. Xen. Orch. 1:117. 1858.
Stanhopeastrum ecornutum Rchb. f. Xen. Orch. 1:124. 1858.
2. Stanhopea pulla Rchb. f. in Gard. Chron. 7:810. 1877. (Fig. 7).
3. Stanhopea cirrhata Lindl. in Journ. Hort. Soc. 5:37. 1850. (Fig. 8).
4. Stanhopea tricornis Lindl. in Journ. Hort. Soc. 4:236. 1849. (Fig. 9).
†*Stanhopea stenochila* Lehm. & Kranzl. in Gard. Chron. 369. 1900.
†*Stanhopea langlasseana* Cogn. in Gard. Chron. 426. 1901.
Stanhopea convulata Rolfe, in Kew Bull. 366. 1909.
5. Stanhopea reichenbachiana Roezl. ex Rchb. f. in Gard. Chron. 2:40. 1879. (Fig. 10).
Stanhopea amesiana Hort. ex Gard. Chron. 352. 1893.
†*Stanhopea lowii* Rolfe, in Kew Bull. 63. 1893.
Stanhopea suavis Hort. in Ospina, Orquidas Colomb.
6. Stanhopea grandiflora (Lodd.) Lindl. Gen. & Sp. Orch. 158. 1832. (Fig. 11).
Ceratochilus grandiflorus Lodd. in Bot. Cab. *t. 1414*. 1828.
Stanhopea eburnea Lindl. in Bot. Reg. 18: *t. 1529*. 1832.
Stanhopea calceolata Hort. ex Rchb. f. 1:117. 1858.
Stanhopea calceolata Drap. Lenq. Hort. Univ. 2:127 & 264.
†*Stanhopea candida* Barb. Rodr. Gen. Spec. Orch. Nov. 1:101. 1877.
Stanhopea randii Rolfe, in Kew Bull. 363. 1894.
7. Stanhopea rodigasiana Claes. ex Cogn. in Gard. Chron. 14. *Fig. 9*. 1898. (Fig. 12).
8. Stanhopea lewisae Ames & Correll, in Bot. Mus. Leafl. Harv. Univ. 10^4:86. Pl. 10. 1942. (Fig. 13).
9. Stanhopea connata Kl. in Otto & Deitz. Alleg. Gartenz. 22:226. 1854. (Fig. 14).
Stanhopea graveolens Kl. ex Rchb. f. Xen. Orch. 1:118. 1879

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* The names placed in synonymy in this list have been previously reduced by other authors with the exception of those marked thusly: †.

10. "*insignis* complex"

STANHOPEA INSIGNIS Frost ex Hook. in Bot. Mag. *t. 1948 & 1949.* 1829. (Fig. 15).

Stanhopea flava Lodd. ex Beer. Prakt. Stud. Fam. Orch. 312. 1854.
Stanhopea atropurpurea Lodd. ex Planch. Hort. Donat. Orch. 215. 1858.
Stanhopea odoratissima Hort. ex Planch. Hort. Donat. Orch. 216. 1858.
Stanhopea macrochila Lem. in Illustr. Hort. 4: Misc. 71. 1859.

STANHOPEA TIGRINA Batem. ex Lindl. Sert. Orch. 1. 1838. (Fig. 16).

Stanhopea cavendishii Lindl. ex Batem. Lond. Hort. Brit. Suppl. 3:643.
Stanhopea maculosa Knowles & Westc. Flor. Cab. 3: *t. 121.* 1839.
Stanhopea nigroviolacea Morren. ex Beer. Prakt. Orch. 313. 1854.
Stanhopea expansa P. N. Don. Hort. Cantab. 13:721. 1845.
Stanhopea lyncea P. N. Don. Hort. Cantab. 13:608. 1845.

STANHOPEA DEVONIENSIS Lindl. Sert. Orch. *t. 1.* 1838.

STANHOPEA MARTIANA Batem. ex Lindl. in Bot. Reg. 26: Misc. 50. 1840. (Fig. 17).

Stanhopea velata Morren, in Ann. Soc. Gand. 3. *t. 153.* 1847.

STANHOPEA SACCATA Batem. Orch. Mex. & Guatem. *t. 15.* 1839.

Stanhopea implicata Westc. ex Lindl. Fol. Orch. Stan. 6. 1852.
Stanhopea radiosa Lem. Illustr. Hort. 4: Misc. 72. 1859.
Stanhopea marshii Rchb. f. Xen. Orch. 1:120. 1879.
Stanhopea elegantula Rolfe, in Kew Bull. 161. 1910.

STANHOPEA INTERMEDIA Kl. in Act. Hort. Petrop. 17:142. 1898.

11. "*oculata* complex"

STANHOPEA OCULATA (Lodd.) Lindl. Gen. & Sp. Orch. Pl. 158. 1832. (Fig. 19).

Ceratochilus oculatus Lodd. in Bot. Cab. *t. 1764.* 1832.
Stanhopea lindleyi Zuccar, Abh. Akad. Muenich 2:320. 1831–33.
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Stanhopea aurea Lodd. ex Lindl. in Bot. Reg. 4: Misc. 11. 1841.
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Species too poorly known to place at present

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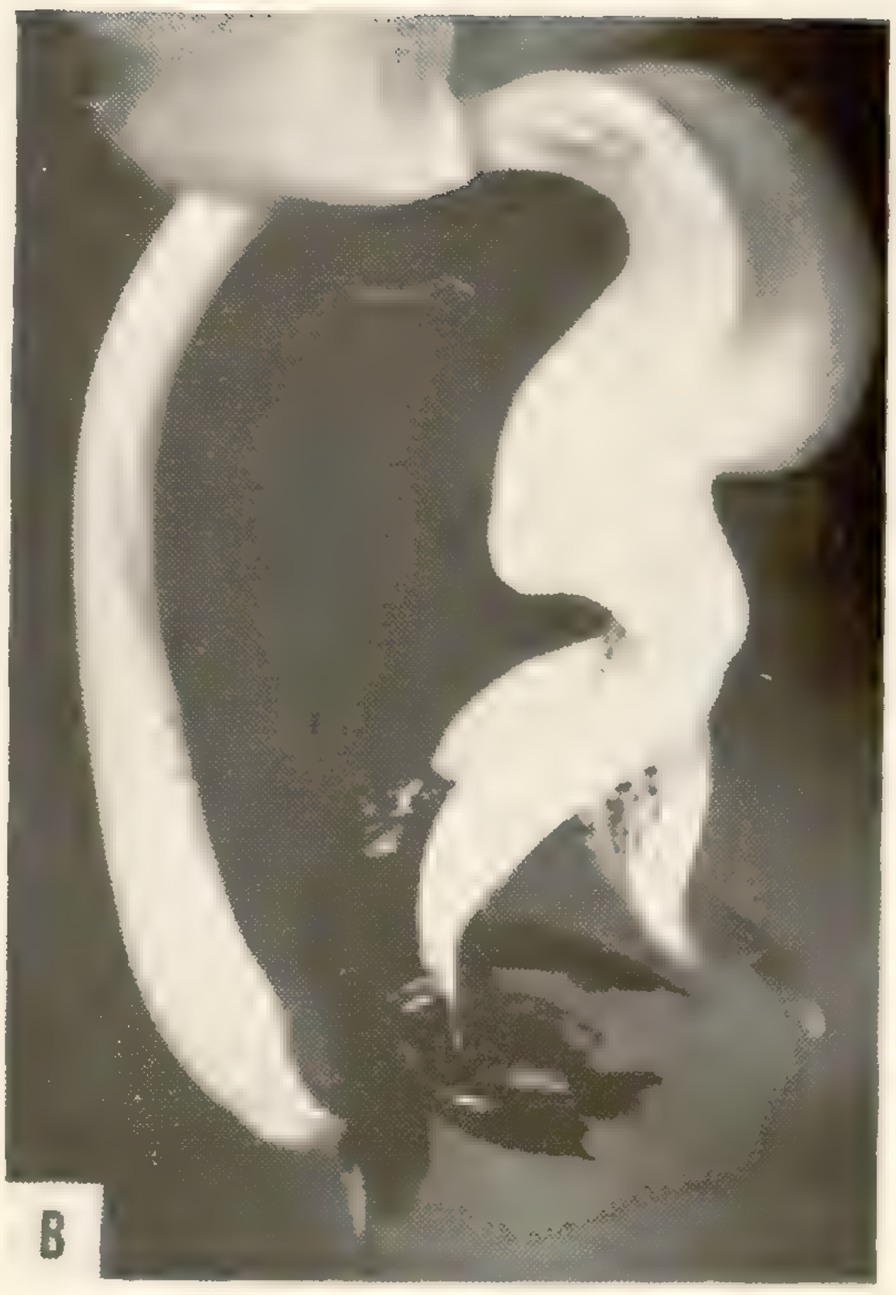
Explanation of Plate

PLATE III

Pollination in *Stanhopea*

A. *Eulaema bomboides* attempting to land on the hypochile of *Stanhopea bucephalus*. B. Bee falling through the flower and engaging the spine of the rostellum under his metathorax. C. Pollinia being inserted into the stigmatic cleft while the bee is falling through the flower. D. *Eulaema moriana* approaching the flower of *S. tricornis*.

A


B

C

D

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PRELIMINARY REVISION OF THE GENUS DRYMARIA

JAMES A. DUKE

Abstract

For the first time since the days of DeCandolle, a revision of all the known species of *Drymaria* is presented. The species are arranged in seventeen series, and keys are provided to the forty-eight species recognized. Illustrations, mostly based on type material, and morphological descriptions are provided for each species. Two new species, **D. barkleyi** and **D. conzattii**, are described, as well as several new infraspecific taxa. JAMES A. DUKE, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

Introduction

The genus *Drymaria* comprised four species at the time of its establishment by Willdenow (in Roem. & Schult. Syst. Veg. 5:406. 1819). Less than 150 years later the number of names has multiplied more than thirty-fold, with most of the novelties being described before the turn of the present century. No complete revision has been attempted since this prodigious multiplication of epithets. Wiggins (in Proc. Cal. Acad. 4^{25}:189. 1944) has completed an able revision of the genus as represented in the vicinity of the Sonoran Desert. His conclusions were quite sound, and the only consequential differences expressed in the present paper are mere matters of heirarchic reduction.

In addition to Wiggins, the most important recent American studies on *Drymaria* have been pursued by Fosberg, who has clarified many of the problems created by M. E. Jones, proposed a few new taxa, and made several appropriate reductions, both in the literature and in various herbaria. Macbride's account in the Flora of Peru, although promulgating a few errors, has been a forward step toward understanding the genus in an unusually complicated region, where speciation in *Drymaria* has run rampant. I. M. Johnston's studies in the equally perplexing Coahuilan Desert have resulted in the description of some of the most bizarre species of *Drymaria*. The major contributor from Europe has been the late Dr. Mattfeld whose discerning work has been responsible for the recognition of several new South American species, all of them herein maintained. He has also clarified some of the errors stemming from the work of his predecessor Briquet, who described several new Mexican species, two of which were probably based upon Pavon's Peruvian collections.

Gross Morphology

An amazing array of characters is exhibited in the genus, and will doubtless tempt the description of minor variants. The petals, for example, are nearly as variable as those of *Silene*. Almost every portion of the plant has been utilized as a taxonomic tool at one place or another in the genus.

Various habits are assumed by members of the genus. Perhaps most common is the clambering and sprawling habit exhibited by *D. cordata*, which occasionally roots at the nodes. Erect suffrutescent perennials are not uncommon, and may raise an eyebrow on those not intimately familiar with the genus. Depressed subcespitose forms such as occur in some varieties of *D. effusa* recall some species of *Arenaria*, while delicate subvirigate annuals such as *D. leptophylla* may suggest *Stipulicida*. Too often, the duration has been used as a key character, but the duration of a plant is frequently a function of the environment. Plants grown in more xeric habitats often exhibit more attributes of a perennial.

Although the leaves of most species are of an ovate type and often cordate at the base, every extreme, from linear and subsucculent to reniform and membranaceous, is found in one species or another. The leaves are usually entire, but undulations occur in the leaf margins of some South American species. The opposite arrangement prevails, but in a few series pseudoverticillate leaves are common. Venation of the leaves is usually obscure and rarely of taxonomic significance, but the texture and pigmentation occasionally aid in identification. The petioles may be as long as the blades or completely obsolete. Most species have stipules which may be entire, bifid, or irregularly lacerate, and the nature of the division is of occasional importance as a taxonomic criterion.

Indumental variations are often called upon for specific delimitations. Septate or moniliform hairs occur in several species. Forms of *D. villosa* may be hirsute or villose in nature; forms of *D. ovata* are best described as lanose; stipitate or sessile glands are present in many species. In *D. cordata* the glands commonly take the form of a conspicuous farinose girdle on the pedicels. The indument is usually more or less translucent, but is not uncommonly white, or even reddish or yellowish. Completely glabrous species occur, and some of the xeromorphic and halophytic species are decidedly glaucous.

Predominating in the genus is a terminal cymose inflorescence, but here again, numerous departures from the norm exist. In most species with the leaves pseudoverticillate, the flowers reflect this arrangement. Rarely the flowers may be solitary or clustered in the axils of barely modified leaves, but more commonly each flower is subtended by more or less scariose bracts. Many inflorescences show racemose tendencies; in *D. anomala*, the first and sometimes the second branches of the inflorescence are dichasial, but subsequent branching tends to be monopodial. Proportionate lengths of bracts, pedicels, peduncles and flowers, as well as relative variations in their induments, have been used in distinguishing species.

Almost invariably there are five sepals in a flower, but aberrant flowers are known with four or six sepals. The sepals are most commonly lanceolate or ovate but in some they are nearly orbicular and in others nearly deltoid. One to nine nerves may traverse each sepal, the 3-nerved sepal being most prevalent. In some

few species the venation is more or less dendritic and in others so obscure as to be difficult of interpretation. Occasionally the sepals are conspicuously carinate or cucullate. Shape, apex, nervation, indument and comparison of the sepals are frequent taxonomic tools.

Petals are usually five in number, but three is characteristic of certain species, and the petals are absent or drastically reduced in *D. apetala* and in forms of *D. villosa* and *D. xerophylla*. Typically the petal is bifid for about half its length, but this basic construction is hard to visualize in some of the members of the first few series whose ornate petals are so bizarre as to defy terse terminology to describe them. The lobes in some more easily described forms are merely basally auriculate, the nature of the auricles being quite variable, as are the venation and apices of the lobes. Most of the bilobed petals are tapered directly to a narrow claw, but in some members (e.g. in Series FASCICULATAE) there is a longer or shorter trunk interpolated between the lobes and the claw. In some forms (e.g. Series HOLOSTEOIDES) the trunk never narrows to a claw; such forms are herein referred to as exunguiculate. The lobes of the bilobed petals are 1–many-nerved, the 1-nerved condition being characteristic of the Series CORDATAE, and certain species in other series.

Less constant in number than the petals are the stamens, which are occasionally reduced to two in number. In species with the reduced stamen number, the anthers are often abortive, and tend to be more orbicular than in those species possessing the higher number of stamens; in pentandrous flowers the anthers are usually oblong. Not infrequently the filaments are shallowly connate into a cup, and there are occasionally minute staminodial flaps alternating with the filaments on such a cup. Rarely, as in *D. stipitata*, there are conspicuous saccate staminodia. In the Series FRUTESCENTES occasionally floral dimorphism suggests that monoecism is in the early stages of evolution.

Offering little in the way of systematic clues is the gynoecium. In a few species the ovary is borne at the summit of a rather prominent stipe, the presence of which does not seem to be necessarily constant. Some species, which are also characterized by the development of staminodia, have a rather prominent stylopodium atop the ovary. In most species, there are three styles, but occasionally there may be two or four. Such numerical variations have been observed in a single inflorescence. The degree of fusion of the styles on the other hand seems to be a more reliable taxonomic criterion, the styles being fused to a greater or lesser degree in most species. Only with hesitancy do I use the word *fused*; it would seem to be just as well to speak of one style with three branches as to speak of three styles partially fused. For the sake of tersity, I have often described the style as being bifid or trifid half its length, when it might have been more correct morphologically to say that there were two or three styles fused for half their length. Interestingly the two or three styles are almost completely free in *D. cordata*, a species which has the most reduced androecium, and a species which I would judge to be one of the most advanced in the genus.

The capsule may be three-valved or two- or four-valved, correlated with the number of styles. Rarely the size of the capsule may be diagnostic. Inside the

capsule, 1–many of the campylotropous ovules may mature into seeds, and the seeds have proven very valuable in the taxonomy of the group. The number, shape, color and sculpture of the seeds all play some part in species determination. Most species are characterized by many-seeded capsules, but in the Series CORDATAE, some occasionally mature only one seed per capsule. The seeds may assume any of several shapes. Perhaps most common is the cochleate, or snail-shaped seed, characteristic of Series CORDATAE. Foetiform seeds, shaped much like the human foetus, are found in the Series HOLOSTEOIDES, and the vestiges of this shape are retained in some subsequent groups. Ampulliform, or retort-shaped, seeds occur in *D. debilis* and this shape is approached by a few species of other sections. The seeds of *D. viscosa* are unusual not only in being lacrimiform, but also in being smooth, dull and yellowish. Many members of the earlier series have hippocrepiform seeds and species of the Series LYROPETALA have hairs on the hump of the horseshoe. Seeds of most species are characterized by various kinds of sculpture. In the earlier series the seeds are merely granular, if we exclude the hairs of Series LYROPETALA from the realm of sculpture. Later sections, especially in the Series VILLOSAE are endowed with species whose seeds are ornate indeed. For example the tubercles in *D. villosa* are stellate in outline, those in its subsp. *palustris* are often capitate, those in *D. divaricata* var. *stricta* are secondarily tuberculate. On the other hand, forms of *D. ovata* have smooth and lustrous black seeds. Usually the seeds are reddish-brown, but in *D. viscosa* they are yellow; occasionally seeds of some species in the Series ARENARIOIDES emit a purple substance into the dissection medium. Seeds have turned out to be rather critical indicators of a species' systematic position in *Drymaria*. It should be pointed out however, that in working with *Spergula*, J. K. New (in Ann. Bot. 23:23. 1960) has found variations in the number of papillae on the seed coats to be environmentally induced. Furthermore she has found no genetic correlation between the variations in seed-coats and in hairiness. Species of *Drymaria*, whose seeds are highly viable a year after collection and germinate rapidly in the greenhouse, should prove interesting subjects for similar studies.

Geography

Departing somewhat from the "typical" picture of the Caryophyllaceae, *Drymaria* is largely a subtropical genus. Of the forty-eight species herein maintained, all but two are strictly American, and only one subspecies does not occur in America. As a whole in America the genus ranges from the western United States through Central and South America to Argentina and Chile, the large majority of the species occuring on the western halves of the continents. Florida, Surinam and Brazil, on the eastern shore, seem to possess only the pantropical *D. cordata*. For a geographical tabulation of species, the reader is referred to the citation of specimens which terminates this paper.

Of particularly geographical interest is *D. cordata*, whose varietal potential and geographical distribution has been studied in some detail by Mizushima (in Jour. Jap. Bot. 32:69. 1957). Almost all material from continental Asia belongs to the subspecies *diandra* (maintained as a species by Mizushima), a subspecies completely

lacking in America (excl. Hawaii). On the Pacific Islands both subspecies and the rather distinct variety *pacifica* occur and appear to maintain their integrity by and large. In Africa however, there are about as many intermediates as there are pure representatives of the two subspecies.

A second species occurs in Malaysia and, to judge from the literature, has been introduced there only within the present century. Of course there is the more remote possibility that it has merely been overlooked until this century. The species, *D. villosa*, is so distinct that I prefer to believe that it is a recent introduction from the Americas.

Several interesting disjunctions are apparent in the genus. Most striking is that illustrated by *D. ladewii*, known only from two collections in Bolivia, but represented by bountiful material from Guatemala and southern Mexico. More easy of interpretation are several vicarious disjunctions between Baja California and mainland Mexico, e.g. *D. holosteoides* & *D. pachyphylla*; *D. arenarioides* ssp. *peninsularis* & *D. arenarioides* ssp. *arenarioides*; *D. gracilis* ssp. *carinata* & *D. gracilis* ssp. *gracilis*.

Economics

Often a conspicuous element in the herbaceous vegetation, *Drymaria* probably plays in the subtropics the insignificant role played by the chickweed in temperate North America, fairly well known, but hardly a topic for conversation. *Drymaria cordata*, and perhaps others, which spread radially and root at the nodes forming rather lush mats, have been planted as ground covers. In Ecuador various species are used as curatives for liver and kidney ailments. In Mexico, species are reputedly used to cure "yaza" and in the Orient, infusions are purportedly used to alleviate headaches. One should be careful of the plant, especially as an oral administration. *Drymaria pachyphylla* (and probably related species) is seriously toxic to livestock, and all measures should be taken to prevent its spread in the arid West, where palatable fodder is at a minimum. Fortunately the seeds alone of *D. pachyphylla* are so distinctive (see Fig. 1C) as to separate it from any other species.

Acknowledgments

In the course of this study I have been fortunate enough to study all or most of the material of the Gray Herbarium, the University of California, the New York Botanical Garden, the Field Museum, the Pomona College Herbarium, the Missouri Botanical Garden, the Rijksherbarium, the Leningrad Herbarium, the Herbarium of the University of Glasgow, the Botanisches Museum of Berlin, the Botanische Staatssammlung at Munich, the Museum National d'Histoire Naturelle at Paris, and the University of Michigan. Critical material has also been loaned by the curators of the herbaria at Kew, Prague, Stockholm, Lija, Lund, Geneva, Göttingen, the University of Brazil, and the California Academy of Sciences. Dr. Ramón Ferreyra has forwarded many interesting Peruvian specimens for determination. To him and to the curators and my correspondents at all the aforementioned institutions, I express my sincere gratitude for making their time and efforts available to me. To my colleagues here at the Missouri Botanical Garden, I am indebted

for their suggestions and comments.* Special thanks are extended to my wife, Peggy, who has been kind enough to prepare the illustrations.

DRYMARIA Willd.

DRYMARIA Willd. ex Roem. & Schult. Syst. 5:31. 1819.

Pinosia Urban, in Arkiv. Bot. 23A[5]:70. pl. 2. 1930.
Mollugophytum M. E. Jones, in Extr. Contr. West. Bot. 18:35. 1933.

Annual or perennial, glabrous or pubescent herbs, occasionally subligneous below, prostrate, spreading or erect. Leaves opposite or pseudoverticillate, glabrous to villose or glandular, sessile to long-petiolate, usually with persistent or fugaceous small stipules. Flowers few to many in dichasial cymes, rarely in pseudoverticils, racemes, or solitary or clustered in the leaf axils. Sepals 5, not connate. Petals (0–) 3–5, white, usually 2-cleft, occasionally appendiculate in the sinus, often auriculate. Stamens 2–5, the anthers versatile, 2-celled, the flattened filaments slightly connate at the base, rarely alternating with prominent staminodia. Ovary superior, slightly stipitate; carpels mostly 3, the 3 styles more or less united below; ovules few to many, campylotropous on free central placentae. Capsule ovoid to spheroid, usually dehiscing into 3 entire valves; seeds 1 to many, cochleate, foetiform, hippocrepiform, or ampulliform, usually tuberculate, the embryo curved about the perisperm.

As here conceived the genus consists of 48 species, all but two of them exclusively American. Since the genus has never been monographed in its entirety, and no supraspecific classification has been elaborated, I would like to propose the following informal series, most of which seem to be rather homogeneous. Following a tabular presentation of the series is an artificial analytic key to all species. Following this is a systematic key to the series. The latter key, although not assuredly phylogenetic, is so set up that species with the more elaborate floral characters, often correlated with certain vegetative factors, come first, and the species with simpler floral construction come later. I am not prepared to say whether evolution in the genus has been a matter of reduction or amplification or both.

SUPRASPECIFIC CLASSIFICATION

A. Series HOLOSTEOIDES
- 1. *D. holosteoides*
- 2. *D. pachyphylla*

B. Series LYROPETALA
- 3. *D. elata*
- 4. *D. subumbellata*
- 5. *D. suffruticosa*
- 6. *D. lyropetala*

C. Series STIPITATAE
- 7. *D. stipitata*

D. Series ARENARIOIDES
- 8. *D. molluginea*
- 9. *D. arenarioides*
- 10. *D. axillaris*
- 11. *D. barkleyi*
- 12. *D. polycarpoides*

E. Series VISCOSAE
- 13. *D. viscosa*

F. Series ORTEGIOIDES
- 14. *D. ortegioides*

*Dr. F. Raymond Fosberg has kindly reviewed an early draft of this paper and made many valuable suggestions; unfortunately Dr. Fosberg's comments were received as this went to press, and could not be used to full advantage.

G. Series EXCISAE

15. *D. hypericifolia*
16. *D. excisa*
17. *D. longepedunculata*

H. Series LEPTOPHYLLA

18. *D. effusa*
19. *D. leptophylla*

I. Series TENUES

20. *D. anomala*
21. *D. tenuis*

J. Series FRUTESCENTES

22. *D. stellarioides*
23. *D. stereophylla*
24. *D. auriculipetala*
25. *D. frutescens*

K. Series FASCICULATAE

26. *D. fasciculata*
27. *D. engleriana*
28. *D. praecox*

L. Series DEBILES

29. *D. debilis*

M. Series LAXIFLORES

30. *D. laxiflora*

N. Series VILLOSAE

31. *D. multiflora*
32. *D. conzattii*
33. *D. malachioides*
34. *D. villosa*

O. Series GRANDIFLORES

35. *D. firmula*
36. *D. ovata*
37. *D. apetala*
38. *D. glaberrima*
39. *D. monticola*
40. *D. grandiflora*
41. *D. paposana*
42. *D. rotundiflora*

P. Series DIVARICATAE

43. *D. divaricata*

Q. Series CORDATAE

44. *D. gracilis*
45. *D. glandulosa*
46. *D. xerophylla*
47. *D. ladewii*
48. *D. cordata*

ARTIFICIAL KEY TO SPECIES AND SUBSPECIFIC TAXA

1. Petals absent or reduced, shorter than the stamens:
   2. Sepals acute:
      3. Plants villose.....34a. D. VILLOSA f. TEPICANA
      3. Plants not villose:
         4. Sepals 3–4 mm. long; Mexico.....46. D. XEROPHYLLA
         4. Sepals 7.5–9.0 mm. long; Peru.....37 D. APETALA
   2. Sepals obtuse.....34b. D. VILLOSA f. TOWNSENDII
1. Petals present; longer than or as long as the stamens:
   5. Petals laterally lacerate, alternating with clavate staminodia.....7. D. STIPITATA
   5. Petals not laterally lacerate; stamodia not clavate:
      6. Leaves pseudoverticillate; petals often distally lacerate; North America:
         7. Seeds dorsally hispidulous; petals bifid or polylacerate apically.
            8. Inflorescence compact, the bracts subcontinguous:
               9. Sepals 3–5 mm. long.....3. D. ELATA
               9. Sepals 5–6 mm. long.....4. D. SUBUMBELLATA
            8. Inflorescence lax, the bracts remote.
               10. Trunk of the petals nearly as broad as long; plants glabrous.....5. D. SUFFRUTICOSA
               10. Trunk of the petals about twice as long as broad; plants glandular.....
                  .....6. D. LYROPETALA
         7. Seeds not dorsally hispidulous; petals bifid or polylacerate apically:
            11. Petals apically 3–many-fid.

12. Leaves linear to oblong; seeds not foetiform.
13. Flowers in cymes, the bracts clearly different from the foliage leaves.....8. D. MOLLUGINEA
13. Flowers more or less racemose, the bracts little different from the foliage leaves.
14. Plants not glandular; petals trifid and bifid.....11. D. BARKLEYI
14. Plants glandular; petals 4–6-fid:
15. Sepals and petals 4–7 mm. long.....9a. D. ARENARIOIDES ssp. ARENARIOIDES
15. Sepals and petals 2.8–4.0 mm. long; Baja California.....9b. D. ARENARIOIDES ssp. PENINSULARIS
12. Leaves more or less elliptic, glaucous; seeds foetiform:
16. Petals with 5–10 lobes; sepals 3–5 mm. long; Baja California.
17. Nodes mostly more than 4 cm. apart, often branching.....1a. D. HOLOSTEOIDES var. HOLOSTEOIDES
17. Nodes mostly less than 4 cm. apart, rarely branching.....1b. D. HOLOSTEOIDES var. CRASSIFOLIA
16. Petals mostly with 4 lobes; sepals 2.0–3.5 mm. long; Continental North America.....2. D. PACHYPHYLLA

11. Petals merely bifid.
18. Sepals obtuse, not strongly 3-ribbed; flowers racemose or cymose.
19. Sepals stipitate-glandular; Baja California.
20. Seeds yellow, smooth.....13. D. VISCOSA
20. Seeds brown, tuberculate or granular.....9b. D. ARENARIOIDES ssp. PENINSULARIS
19. Sepals withont stipitate glands; continental North America:
21. Leaves linear.....8. D. MOLLUGINEA
21. Leaves elliptic.....11. D. BARKLEYI
18. Sepals acute or strongly 3-ribbed, if obtuse, the flowers in cymes.
22. Sepals obtuse (*D. effusa*):
23. Bracts mostly shorter than the pedicels:
24. Axes of the inflorescence stipitate-glandular.....18a. D. EFFUSA var. EFFUSA
24. Axes of the inflorescence not stipitate-glandular.....18b. D. EFFUSA var. CONFUSA
23. Bracts mostly longer than the pedicels; plants minute.....18c. D. EFFUSA var. DEPRESSA
22. Some or all the sepals in a flower acute to acuminate (*D. leptophylla*):
25. Peduncles not stipitate-glandular; pedicels shorter than the bracts.....19a. D. LEPTOPHYLLA var. LEPTOPHYLLA
25. Peduncles stipitate-glandular; pedicels (ultimately) longer than the bracts.
26. Sepals lanceolate, not stipitate-glandular...19b. D. LEPTOPHYLLA var. COGNATA
26. Sepals ovate, stipitate-glandular.....19c. D. LEPTOPHYLLA var. NODOSA

6. Leaves opposite; petals bifid, the lobes themselves sometimes dichotomizing; North and South America, 2 spp. more or less pantropical.
27. Petals 2–many-times dichotomous; Mexico; West Indies:
28. Leaves elliptic; Cuba.....14. D. ORTEGIOIDES
28. Leaves ovate to reniform; Mexico:
29. Plants villose; petals 1–2 times dichotomous.....17. D. LONGEPEDUNCULATA
29. Plants not villose; petals 2–4 times dichotomous:
30. Leaves deltoid-ovate, rather narrow.....15. D. HYPERICIFOLIA
30. Leaves suborbicular to obreniform.....16. D. EXCISA

27. Petals merely bifid, the lobes occasionally emarginate.
31. Leaves linear to elliptic: (cf. also *D. polycarpoides*, *D. axillaris*.)
32. Plants rarely suffruticose; North America.
33. Leaves linear to spatulate; petioles obsolete:
34. Sepals all obtuse, often cucullate (*D. effusa*):
35. Plants more than 5 cm. tall; many of the pedicels longer than the bracts.

36. Peduncles and pedicels stipitate-glandular.....18a. D. EFFUSA var. EFFUSA
36. Peduncles and pedicels not stipitate-glandular.....18b. D. EFFUSA var. CONFUSA
35. Plants mostly less than 5 cm. tall; bracts mostly longer than the pedicels.....18c. D. EFFUSA var. DEPRESSA
34. Some or all of the sepals acute or acuminate (*D. leptophylla*).
37. Peduncles not stipitate-glandular; pedicels mostly shorter than the bracts.....19a. D. LEPTOPHYLLA var. LEPTOPHYLLA
37. Peduncles stipitate-glandular; pedicels often elongate.
38. Sepals lanceolate, not stipitate-glandular.....19b. D. LEPTOPHYLLA var. COGNATA
38. Sepals ovate, stipitate-glandular.....19c. D. LEPTOPHYLLA var. NODOSA
33. Leaves lanceolate, the petioles obvious:
39. Sepals 3-ribbed.....20. D. ANOMALA
39. Sepals 1-ribbed.....21. D. TENUIS
32. Plants suffrutescent; Peru and Ecuador:
40. Leaves neither imbricate nor pungent.
41. Sepals usually glandular, the midrib not excurrent.
42. Leaves subpergameneous, stipitate; Ecuador.....22. D. STELLARIOIDES
42. Leaves membranaceous, often estipulate; Peru.....23. D. STEREOPHYLLA
41. Sepals glabrous, the midrib excurrent.....24. D. AURICULIPETALA
40. Leaves imbricate, pungent.....25. D. FRUTESCENS
31. Leaves narrowly ovate to reniform.
43. Petals exunguiculate, the broad trunk not narrowed to a claw, the trunk about as wide as the combined widths of the lobes.
44. Petal-lobes emarginate.....30. D. LAXIFLORA
44. Petal-lobes acute to emarginate.
45. Cyanic glaucous perennials of the Coahuilan Desert.
46. Flowers axillary, the sepals stipitate-glandular.....10. D. AXILLARIS
46. Flowers cymose, the sepals glabrous.....12. D. POLYCARPOIDES
45. Verdant annuals or perennials of South America.
47. Sepals more than 4.5 mm. long, or the bracts not stipulate..
48. Inflorescences mostly axillary, lax, the pedicels obvious...38. D. GLABERRIMA
48. Inflorescences terminal, dense, the pedicels obscured.....26. D. FASCICULATA
47. Sepals less than 4.5 mm. long, the bracts often stipulate.
49. Sepals acute, stipitate-glandular:
50. Pedicels mostly longer than the bracts.....28. D. PRAECOX
50. Pedicels mostly shorter than the bracts.....27a. D. ENGLERIANA var. ENGLERIANA
49. Sepals acuminate, glabrous.....27b. D. ENGLERIANA var. DEVIA
43. Petals with a definite claw, the two lobes basally tapered or truncate to the claw:
51. Petals with ciliate auricles near the summit of the claw; seeds with substellate or capitate or cylindric tubercles:
52. Leaves broadest at or above the middle, the stipules entire, lanceolate; sepals subdeltoid, widest quite near the base.....31. D. MULTIFLORA
52. Leaves broadest below the middle, the stipules if entire, filiform or acicular; sepals oblong to orbicular; widest well above the base.
53. Sepals 4.5 mm. long or longer; leaves cordate, often broader than 1.5 cm.
54. Stipules longer than the petioles.....32. D. CONZATTI
54. Stipules shorter than the petioles.....33. D. MALACHIOIDES
53. Sepals mostly less than 4.5 mm. long; leaves if rarely cordate, mostly less than 1.5 cm. broad:
55. Plants villose; mostly clambering annuals.
56. Sepals elliptic, acute; tubercles of the seeds stellate.....34a. D. VILLOSA ssp. VILLOSA

56. Sepals oblong to orbicular, obtuse; tubercles of the seeds stellate, capitate, cylindric or simple.
57. Seeds with ornate tubercles; petal lobes not deeply emarginate; sepals usually glabrous.....34b. D. VILLOSA ssp. PALUSTRIS
57. Seeds with simple tubercles; petal lobes deeply emarginate; sepals villosulous.....17. D. LONGEPEDUNCULATA
55. Plants glabrous, the leaves occasionally villose but glabrescent; plants sprawling annuals or erect perennials.....34b. D. VILLOSA ssp. PALUSTRIS
51. Petals without ciliate auricles; seeds with simple or ornate tubercles, rarely etuberculate:
58. Plants villose:
59. Seeds ampulliform; stamens of two sizes; Baja California.....29. D. DEBILIS
59. Seeds cochleate; stamens more or less equal:
60. Seeds with ornate tubercles; sepals no more than 4.5 mm. long:
61. Sepals glabrous, obtuse.....34b. D. VILLOSA ssp. PALUSTRIS
61. Sepals villose or villosulous, obtuse or acute.
62. Sepals obtuse; Venezuela and Colombia.....34c. D. VILLOSA ssp. PARAMORUM
62. Sepals acute; Peru.....28. D. PRAECOX
60. Seeds smooth or the tubercles not ornate; sepals 4–10 mm. long:
63. Petals bifid about ¾ their length, the lobes broad, 7–11-nerved; Peru.....40. D. GRANDIFLORA
63. Petals bifid about ½ their length, the lobes narrow, 3–7-nerved; Andean South America.....36. D. OVATA
58. Plants not villose:
64. Petals equaling or shorter than the sepals, the lobes mostly 1-nerved; stamens often fewer than five:
65. Petals about equaling the sepals in length:
66. Sepals 3-nerved, not carinate; tubercles ornate.
67. Sepals oblong to orbicular, obtuse, the petals often with ciliate auricles; tubercles of the seeds stellate or capitate.....34b. D. VILLOSA ssp. PALUSTRIS
67. Sepals elliptic, acute, the petals scarcely auriculate; tubercles of the seeds domical or conical, secondarily tuberculate.....43b. D. DIVARICATA var. STRICTA
66. Sepals 1-nerved, carinate; tubercles not ornate (*D. gracilis*).
68. Stipules lacerate; continental Mexico and Central America.....44a. D. GRACILIS ssp. GRACILIS
68. Stipules entire; Baja California.....44b. D. GRACILIS ssp. CARINATA
65. Petals shorter than the sepals.
69. Flowers clustered in axils of subsessile leaves, the inflorescence, if rarely proliferating, with supernumerary bracts.....46. D. XEROPHYLLA
69. Flowers in lax terminal and axillary cymes, if rarely solitary, the leaves obviously petiolate.
70. Leaves more or less deltoid, trinerved, with the secondary veins forming an interrupted, slightly raised, reticulum, very thin; stipules entire; Chiapas, Guatemala; Bolivia.....47. D. LADEWII
70. Leaves ovate to reniform or cordate, not obviously trinerved or reticulate; stipules lacerate:
71. Seeds 0.6–0.8 mm. long, the tubercles rectanguloid, remote; plants often erect and perennial.....45a. D. GLANDULOSA var. GLANDULOSA
71. Seeds 0.8–2.0 mm. broad, the tubercles domical, contiguous; plants annual and usually prostrate:
72. Flowers broadest at or below the middle, the sepals not inflexed; seeds 0.8–1.5 mm. broad...48a. D. CORDATA ssp. CORDATA
72. Flowers broadest above the middle, the sepals usually incurved; seeds 1.5–2.0 mm. broad.....48b. D. CORDATA ssp. DIANDRA

64. Petals equaling or exceeding the sepals, the lobes with dendritic or flabellate venation; stamens mostly five:
  73. Sepals obtuse, often cucullate; South America:
    74. Flowers in lax axillary cymes; plants glabrous:
      75. Petals subexunguiculate; Peru.....38. D. GLABERRIMA
      75. Petals tapered to a long definite claw; Galapagos Islands.....39. D. MONTICOLA
    74. Flowers in dense to lax, mostly terminal, cymes:
      76. Sepals glandular or villosulous:
        77. Sepals carinate, the inflorescences capitate:
          78. Petals clearly exerted, the lobes truncate to the claw; Peru.....41b. D. PAPOSANA var. WEBERBAUERI
          78. Petals little if at all exerted, the lobes tapered to the claw; northern Chile.....41a. D. PAPOSANA var. PAPOSANA
        77. Sepals not or rarely carinate, the inflorescences lax.....40. D. GRANDIFLORA
      76. Sepals glabrous or with scanty sessile glands:
        79. Sepals ellipsoid to orbicular, quite obtuse, often with sessile glands.....42a. D. ROTUNDIFOLIA var. ROTUNDIFOLIA
        79. Sepals narrowly to broadly ovate, acutish, glabrous.....42b. D. ROTUNDIFOLIA var. NITIDA
  73. Sepals acute; North and South America:
    80. Seeds lustrous, often smooth; leaves often pergameneous:
      81. Stipules as long as the petioles; seeds tuberculate; Venezuela.....35. D. FIRMULA
      81. Petioles equaling to much longer than the stipules; seeds corrugated or smooth; Colombia to Argentina along the Andes.....36. D. OVATA
    80. Seeds dull, tuberculate; leaves membranaceous:
      82. Seeds with low remote tubercles; Mexico.....45b. D. GLANDULOSA var. GALEOTTIANA
      82. Seeds with prominent, often contiguous, tubercles; South America:
        83. Sepals carinate, the carinae often serrulate
          84. Inflorescence capitate, the petal lobes truncate to the claw.....41b. D. PAPOSANA var. WEBERBAUERI
          84. Inflorescence lax, the petal lobes tapered to the claw.....41c. D. PAPOSANA var. SERRULATA
        83. Sepals rarely carinate, the carina not serrulate:
          85. Inflorescence capitate, the petal lobes truncate to the claw.....41b. D. PAPOSANA var. WEBERBAUERI
          85. Inflorescence not capitate, the petal lobes tapered to the claw but often auriculate:
            86. Petals and sepals about equal in length:
              87. Petals auriculate:
                88. Sepals weakly nerved, basally saccate:
                  89. Leaves long-petiolate; tubercles of the seeds mammiliform.....43a. D. DIVARICATA var. DIVARICATA
                  89. Leaves short-petiolate; tubercles of the seeds secondarily tuberculate.....43b. D. DIVARICATA var. STRICTA
                88. Sepals strongly nerved, not basally saccate:
                  90. Leaves elliptic to ovate, short-petiolate.....43e. D. DIVARICATA var. REFLEXIFLORA
                  90. Leaves, at least some on a given plant, reniform, long-petiolate:
                    91. Sepals and herbage densely viscid-glandular; flowers at anthesis ca. twice as long as broad,

rather square in cross section, alpine plant.....
.....44c. D. DIVARICATA var. VISCIDULA

91. Sepals and herbage subglabrous to villosulous; flowers at anthesis broader, terete; loma plants.
.....43d. D. DIVARICATA var. DIVERGENS

87. Petals exauriculate:

92. Minute plants, the pedicels about as long as the bracts; tubercles of the seeds simple.....28. D. PRAECOX

92. Large plants, the pedicels much longer than the bracts; tubercles of the seeds secondarily tuberculate.....43b. D. DIVARICATA var. STRICTA

86. Petals much longer than the sepals:

93. Petals exauriculate:

94. Seeds lustrous.....36. D. OVATA

94. Seeds not lustrous:

95. Plants glabrous:

96. Leaves long-petiolate; sepals basally saccate.....
.....43a. D. DIVARICATA var. DIVARICATA

96. Leaves subsessile; sepals not saccate:

97. Sepals strongly nerved, carinate; leaves often crenulate.....
.....41c. D. PAPOSANA var. SERRULATA

97. Sepals weakly nerved, ecarinate; leaves entire.....42b. D. ROTUNDIFOLIA var. NITIDA

95. Plants villose or villosulous.....40. D. GRANDIFLORA

93. Petals auriculate.

98. Plants not villose or villosulous:

99. Leaves subsessile, often crenulate.....
.....41c. D. PAPOSANA var. SERRULATA

99. Leaves long-petiolate, entire.....
.....43a. D. DIVARICATA var. DIVARICATA

98. Plants villose or villosulous.

100. Leaves sessile or subsessile.....40. D. GRANDIFLORA

100. Leaves long-petiolate.....
.....43a. D. DIVARICATA var. DIVARICATA

KEY TO THE SERIES OF DRYMARIA

a. Leaves estipulate, pseudoverticillate, as the flowers; petals with 4–10 distal lobes; seeds foetiform or hippocrepiform, not dorsally hispid.....Series A: HOLOSTEOIDES (p. 186)

a. Leaves, if pseudoverticillate, stipulate; seeds, if foetiform, dorsally hispid:

b. Leaves linear; plants upright perennials; petals with many distal lobes; seeds foetiform, dorsally hispid.....Series B: LYROPETALA (p. 189)

b. Leaves linear to reniform; plants annual or perennial; petals entire to multilobate; seeds, if rarely foetiform, not dorsally hispid:

c. Leaves elliptic, opposite, estipulate; petals apically and laterally polylacerate, alternating with conspicuous clavate staminodia.....Series C: STIPITATAE (p. 193)

c. Leaves and petals various; staminodia neither conspicuous nor clavate:

d. Petals distally 3–8-lobed, or bifid, if merely bifid, the trunk much longer than the claw, laterally denticulate; seeds smooth to granular; North America.....
.....Series D: ARENARIOIDES (p. 193)

d. Petals merely bifid, or equally quadrifid, the lobes sometimes emarginate or dichotomizing; seeds tuberculate (ex. *D. viscosa* and *D. ovata*):

e. Leaves linear, pseudoverticillate or rarely opposite, viscous; seeds smooth; dorsally brown, facially transparent, revealing the yellowish embryo. Baja California.....
.....Series E: VISCOSAE (p. 200)

e. Leaves linear to reniform; opposite, glabrous to villose or glandular; seeds tuberculate (except *D. ovata* var.) reddish brown to black.

f. Petals with four equal lobes or with two dichotomizing lobes. Cuba and Mexico.

g. Stamens and petals three, the petals with four equal lobes; bracts more or less imbricate. Cuba.....Series F: ORTEGIOIDES (p. 200)

g. Stamens and petals five, the petals bifid, the lobes dichotomizing; bracts remote. Mexico.....Series G: EXCISAE (p. 201)

f. Petals merely bifid, the lobes rarely emarginate:

h. Leaves linear to lance-elliptic (ovate in *D. fasciculata*), stipulate or estipulate, petals exauriculate, often exunguiculate; seeds without ornate tubercles.

i. Petals unguiculate; delicate cespitose or erect virgate annuals, rarely spreading and perennial. North America:

j. Leaves linear to oblong or spatulate, the petioles obsolete; plants not laxly spreading.....Series H: LEPTOPHYLLA (p. 204)

j. Leaves lanceolate to elliptic, the petioles evident; plants laxly spreading. .....Series I: TENUES (p. 210)

i. Petals exunguiculate or subexunguiculate; suffrutescent erect perennials or delicate annuals. Peru and Ecuador.

k. Large-flowered suffrutescent perennials, the leaves occasionally estipulate; flowers occasionally dimorphic.....Series J: FRUTISCENTES (p. 212)

k. Small-flowered delicate annuals (exc. *D. fasciculata* which may tend to become large-flowered and suffruticose); leaves stipulate; flowers monomorphic.....Series K: FASCICULATAE (p. 216)

h. Leaves ovate to reniform, stipulate; petals (rarely absent) unguiculate, often auriculate; seeds occasionally with ornate tubercles, rarely smooth and lustrous.

l. Villose plants with long-petiolate leaves; petals simply bifid, exceeding the sepals; stamens 5, all fertile, unequal. Baja California...Series L: DEBILES (p. 220)

l. Glabrous to villose plants with sessile to long-petiolate leaves; petals bifid, the lobes sometimes emarginate or auriculate; stamens 2–5, if unequal, the inequality usually due to sterilization.

m. Trunk of the petals longer than the claw, the lobes deeply emarginate, exauriculate. Western U. S. to Central America.....Series M: LAXIFLORES (p. 222)

m. Trunk of the petals shorter than the claw (except *D. glaberrima*), the lobes acute to emarginate, occasionally basally auriculate:

n. Lobes of the petals mostly with more than one vein, often basally dentate or auriculate, the auricles often ciliate; petals (except in apetalous forms) equaling or exceeding the sepals; seeds usually numerous, with coarse ornate tubercles, or the tubercles simple (absent in *D. ovata*); stamens 5 with oblong anthers, the styles mostly three, joined half their length or more; plants often villose with jointed hairs:

o. Petals basally provided with ciliate auricles (except in forms of *D. villosa* with obtuse often cucullate sepals); tubercles of the seeds stellate, cylindric or capitate; North and South America; introduced in Malaysia.....Series N: VILLOSAE (p. 223)

o. Petals exauriculate or the auricles not ciliate; tubercles of the seeds domical, conical, or rarely secondarily tubercululate; western South America:

p. Inflorescences often subcapitate, the pedicels if longer than the flowers not divaricate; sepals often obtuse, not basally saccate; often carinate; petals often with no trace of an auricle; leaves often sessile, occasionally crenulate, pergameneous, a/o densely villose; Colombia to Argentina.....Series O: GRANDIFLORES (p. 230)

p. Inflorescences lax, the pedicels elongate and divaricate; sepals acute or basally saccate, not carinate; petals with minute deltoid or mammiliform auricles; leaves short- to long-petiolate, entire, membranaceous, not densely villose.....Series P: DIVARICATAE (p. 240)

n. Lobes of the petals 1-nerved (except *D. glandulosa* var. *galeottiana*), exauriculate, the petals mostly shorter than the sepals (except in *D. gracilis* which occasionally has deltoid auricles); seeds 1–many, tuberculate, the tubercles low and domical or rectanguloid, contigu-

ous or remote; stamens and styles often reduced to 2, the anthers then tending to be orbicular, and the styles free nearly to their base; plants not villose.....Series Q: CORDATAE (p. 245)

A. Series HOLOSTEOIDES

Leaves elliptic, pseudoverticillate, estipulate, often somewhat glaucous and succulent. Flowers in pseudoverticils. Sepals obtuse, often somewhat cucullate, the venation subdendritic. Seeds foetiform or hippocrepiform, merely granular, occasionally gibbose and umbonate. Two halophytic species of western United States and Mexico, both probably toxic to cattle. Fig. 1.

a. Sepals 3–5 mm. long; petals 5–10-lobed; seeds 0.6–1.0 mm. long, about as broad as long; herbage glaucous, glabrous or glandular; Baja California:

b. Leaves and stems often stipitate-glandular; many, if not all, the internodes longer than 4 cm., with branching at most of the nodes; petals 2.8–3.5 mm. long, often equaling or exceeding the sepals; seeds often strongly umbonate and gibbose.....1a. D. HOLOSTEOIDES var. HOLOSTEOIDES

b. Leaves and stems glaucous, rarely stipitate-glandular, often tinted with anthocyanins; most of the internodes shorter than 4 cm., with branching at few of the nodes; petals 2.0–3.5 mm. long, the sepals usually longer; seeds rarely gibbose.....1b. D. HOLOSTEOIDES var. CRASSIFOLIA

a. Sepals 2.0–3.5 mm. long; petals 4-lobed; seeds 1.0–1.8 mm. long, about twice as long as broad; herbage glabrous; continental Mexico and adjacent United States.....2. D. PACHYPHYLLA

1a. DRYMARIA HOLOSTEOIDES var. HOLOSTEOIDES

Drymaria holosteoides Benth. Bot. Voy. Sulph. 16. 1844. (HOLOTYPE: *Hinds s. n.* in 1841 at Magdalena Bay; K!; isotypes at GH & LE.)
Drymaria veatchii Curran, in Proc. Cal. Acad. 2^1:227. 1888. (HOLOTYPE: Veatch in 1888 on Cedros Island, UC!)
Mollugophytum holosteoides M. E. Jones, Extr. Contr. West. Bot. 18:35. 1933.

Radially spreading herbaceous to lignescent annuals to as much as 40 cm. long, branching at nearly every node, stipitate-glandular to glabrescent, the internodes mostly much longer than the leaves, with a caducous rosette of spatulate leaves. Cauline leaves pseudoverticillate, the blades glabrous or scantily glandular, occasionally somewhat glaucous, narrowly to broadly elliptic, apically rounded or acutish, basally acute, 4–12 mm. long, 2–7 mm. broad, the petioles glabrous to stipitate glandular, 2–8 mm. long; stipules absent. Inflorescences of terminal and axillary contracted umbelloid cymes, subtended by both normal foliage leaves and scariose ovate bracts 1–2 mm. long; pedicels 2–6 mm. long, glandular or stipitate-glandular. Sepals 5, glandular or stipitate-glandular, broadly oblong, obovate or suborbicular, apically obtuse and often cucullate, 3–4 mm. long, 1.6–3.0 mm. broad, the venation obscure, dendritic; petals 5, 2.8–3.5 mm. long, bifid for about half their length, with 4–6 laciniae in the cleft, these about half as long as the oblong lobes, the trunk suborbicular, denticulate or crenulate, cordate or truncate to the minute claw; stamens 5, ca. 3 mm. long, the oblong anthers ca. 0.6 mm. long; ovary at anthesis globose, the styles attaining the anthers, bifid or trifid less than a third of its length. Capsule subglobose, 1.5–3.0 mm. long, 6–20-seeded, the seeds foetiform, basally umbonate, laterally gibbose and often dorsally flanged, granular, 0.5–

Fig. 1: A. *D. holosteoides* var. *holosteoides* (holotype of *D. veatchii*); petal, 7½×; sepal, 7½×; seed 15×. B. *D. holosteoides* var. *crassifolia* (holotype); petal, 10×; sepal, 10×; seed, 15×. C. *D. pachyphylla* (holotype) petal, 10×; sepal, 10×; stamen, 10×; seed, 10×; habit, ½×.

1.0 mm. long, nearly or quite as broad as long. Fig. 1A (Holotype of *D. veatchii*).

Sandy soils of Baja California, Mexico, mostly north of Cape San Lucas.

The isotype at Leningrad has unusually long styles to 2 mm. long which are divided less than one-third their length, a character more frequent in the var. *crassifolia*. Indeed the type is in some other respects (as well as aspect) intermediate between these closely related varieties but by far the majority of its characteristics are those of the more northern populations. Among other intermediate specimens which forced me to reduce the following species to a variety may be cited *Constance 3185*, which in its strongly gibbose seeds and stipitate-glandular stems approaches the typical variety. However the specimen seems to possess more characteristics of var. *crassifolia*, e. g. the petals are much shorter than the sepals, the internodes are relatively short and the plant is obviously a perennial.

1b. Drymaria holosteoides var. **crassifolia** (Benth.) J. Duke comb. & stat. nov.

Drymaria crassifolia Benth. Bot. Voy. Sulph. 16. 1844. (holotype: *Hinds s. n.* in 1841; Cape San Lucas; K !; isotypes at GH, LE !)

Mollugophytum crassifolium M. E. Jones, Extr. Contr. West. Bot. 18:35. 1933.

Subcespitose herbaceous to lignescent perennials verticillately branching but rarely branching at every node, glabrous or very rarely stipitate-glandular, to as much as 20 cm. long, some of the internodes occasionally shorter than the leaves, with a caducous rosette of spatulate leaves, the taproot to 8 mm. broad. Cauline leaves pseudoverticillate, the blades glabrous, carnose, glaucous, often cyanic, narrowly to broadly elliptic, 4–12 mm. long, 3–8 mm. broad, the petioles 4–12 mm. long, glabrous or glandular; stipules absent. Inflorescences of terminal and axillary contracted umbelloid verticils subtended by normal foliage leaves and by bracts 1–2 mm. long; pedicels 5–12 mm. long, glabrous to stipitate-glandular. Sepals 5, glabrous to scantily sessile-glandular, broadly oblong to elliptic, apically obtuse and often cucullate, 3.0–4.5 mm. long, 1.5–2.5 mm. broad, the venation obscure, dendritic; petals 5, 2.0–3.5 mm. long, bifid for about half their length, with 4–6 laciniae in the cleft, these about half as long as the main lobes; trunks ovate, denticulate, cordate or truncate to the minute claw; stamens 5, ca. 3 mm. long, the oblong anthers ca. 0.6 mm. long; ovary at anthesis subglobose, the styles attaining the anthers, bifid or trifid less than a third of their length. Capsule subglobose to ovoid or ellipsoid, 3–5 mm. long, 7–20-seeded, the seeds hippocrepiform, granular, scarcely umbonate or gibbose, 0.8–1.0 mm. broad, nearly or quite as long as broad. Fig. 1B. (Holotype).

Saline soils around Cape San Lucas, Baja California, Mexico.

2. DRYMARIA PACHYPHYLLA Wooton & Standl. in Contr. U. S. Nat Herb. 16: 121. 1913. (HOLOTYPE: *Wooton 405*, dry plains south of the White Sands, N. Mex., US; isotypes at F, GH, MO, UC, etc.!)

Glaucous subsucculent annuals, the vegetative branching largely confined to radially diverging branches from a slender yellowish rootstock or to terminal pseudoverticillate branch systems, the elongate spreading internodes much exceeding the terminally crowded leaves. Leaves pseudoverticillate, glaucous, subsucculent, wrinkling in drying, broadly elliptic to suborbicular, apically obtuse or acutish, basally tapering to the petiole, 4–14 mm. long, 4–12 mm. broad, the glabrous petioles 4–8 mm. long; stipules absent, the petioles clasping. Inflorescences of terminal and axillary contracted umbelloid verticils subtended by normal foliage leaves and bracts 0.5–1.5 mm. long, the pedicels 1–5 mm. long, the bracts ovate, obtuse, scariose and almost nerveless. Sepals 5, subequal, glabrous, glaucous, ellipsoid, obtuse, 2.5–3.3 mm. long, 1.5–2.0 mm. broad, obscurely 3–5-nerved, the central portion green, the margins scariose; petals 5, 2.5–3.0 mm. long, bifid about half their length, with 2 oblong laciniae in the cleft, the trunk serrulate, tapered to the base, the claw not clearly delineated; stamens 5, 1.0–1.5 mm. long, the oblong anthers ca. 0.5 mm. long; ovary at anthesis subglobose, the short style bifid or trifid more than half its length, slightly exceeding the anthers. Capsule subglobose, 3–4 mm. long, mostly exceeding the sepals, 15–25-seeded, the seeds vermiculiform, facially gibbose, more or less tessellate, 0.8–1.8 mm. long, ca. twice as long as broad. Fig. 1C (Holotype).

Heavy saline soils in denudated or ruderal sites, often as a pioneer on bare areas, western U. S. A. and northern Mexico.

Although certain authorities have regarded this species as synonymous with *D. holosteoides*, there seems to be no justification for such a conclusion, as the mainland species differs constantly in many respects from the preceding species of Baja California. The seed alone would suffice to distinguish this species from all other species of *Drymaria*.

Little (in Ecology 18:416. 1937), who regards *D. pachyphylla* as a synonym of *D. holosteoides*, presents some very interesting information about the ecology and toxicity of this serious weed. All the aerial portions of the plant are toxic to cattle and sheep. To complicate matters, the xeromorphic nature of the leaves is responsible for a degree of resistance to drought and to chemical sprays. Campbell (in Journ. Agr. Res. 43:1027. 1931) has shown the species to be a pioneer in plant succession on clay soils such as the adobe soils of portions of our western ranges.

B. Series LYROPETALAE

Leaves linear, pseudoverticillate, estipulate or with entire caducous stipules. Flowers in pseudoverticils or in cymes. Sepals obtuse or acute, the venation subdendritic. Petals apically 6–14-lobed, laterally denticulate, minutely unguiculate. Seeds hippocrepiform or foetiform, dorsally hispidulous, etuberculate. Four gypsophytic species of the Coahuilan Desert of northeastern Mexico. Fig. 2.

a. Inflorescence pseudoverticillate, compact, the bracts mostly contiguous; petals mostly 6–8-lobed, the lobes lance-deltoid, attenuate, about half as long as the trunk, the trunk occasionally bilinguate; staminodia ligular or obsolescent; stylopodium obsolescent; leaves 10–70 mm. long, without true stipules (suppressed branches or leaves *inside* the leaf bases may be confused with stipules):

b. Sepals 3.0–4.5 mm. long, often glandular; petals 2.5–3.5 mm. long; stamens 2–3 mm. long, the ligular staminodia 0.2–0.5 mm. long, 0.5–0.8 mm. broad; bracts 0.5–1.5 mm. long.....3. D. ELATA

b. Sepals 5–6 mm. long, glabrous or bullate; petals 4.5–6.0 mm. long; stamens 3–5 mm. long, the staminodia obsolete or absent; bracts 2.5–4.0 mm. long.....4. D. SUBUMBELLATA

a. Inflorescence cymose, lax, the bracts remote; petals 10–14-lobed, the lobes linear, obtuse, the outer nearly or quite as long as the trunk, the trunk elinguate; staminodia cupular; stylopodium conspicuous in submature capsules; leaves 3–30 mm. long, with minute caducous stipules:

c. Hairs on the seeds dense, erect, 0.3–0.5 mm. long; trunk of the petals nearly as broad as long, basally tapered to the claw, the apical laciniae subequal in length; leaves 6–30 mm. long; bracts 3–5 mm. long; plants glabrous.....5. D. SUFFRUTICOSA

c. Hairs on the seeds scanty, semi-appressed, 0.2–0.3 (–0.5) mm. long; trunk of the petal nearly twice as long as broad, basally cordate or truncate, the apical laciniae strongly dissimilar; bracts 0.5–3.5 mm. long; plants glandular.....6. D. LYROPETALA

3. DRYMARIA ELATA I. M. Johnston, in Jour. Arn. Arb. 21:68. 1940. (HOLOTYPE: *I. M. Johnston 7823*; 10 km. s. of Laguna del Rey, locally abundant in gypsum silt; Coahuila. GH!)

Upright lignescent perennials, the branches opposite or pseudoverticillate, glabrous or glaucous to stipitate-glandular, the internodes mostly longer than the leaves, the tap root to 1 cm. thick. Leaves opposite or pseudoverticillate, glabrous or glaucescent, succulent, obscurely veined, linear, apically obtuse, 1–7 cm. long, 0.5–1.5 mm. broad. Inflorescences of terminal contracted 5–13-flowered umbelloid cymes, the peduncles mostly 5–8 cm. long, glabrous; bracts 0.5–1.0 mm. long,

Fig. 2: A. *D. elata* (holotype); petal, 10×; sepal, 10×; seed 15×. B. *D. subumbellata* (holotype); petal, 6×; sepal, 6×; seed, 15×. C. *D. suffruticosa* (holotype); petal, 5×; sepal, 5×; stamen, 5×; seed, 15×. D. *D. lyropetala* var. *lyropetala* (holotype); petal, 7½×; sepal, 7½×; stamen, 7½×; seed, 10×. E. *D. lyropetala* var. *coahuilana* (holotype); petal, 7½×; sepal, 7½×; seed, 15×; habit, ½×.

deltoid-ovate, the mature pedicels 4–7 mm. long, puberulent or stipitate-glandular, the outer ones spreading or deflexed. Sepals 5, 3.0–4.5 mm. long, 2–3 mm. broad, stipitate-glandular or glabrate, broadly ellipsoid to suborbicular, apically obtuse, the venation obscure, with 7–9 veins arising from the base, all but the midrib dichotomizing; petals 5, 2.5–3.5 mm. long, with about 6 subequal apical laciniae, these lance-deltoid, falcate, attenuate, and denticulate, the trunk longer than the laciniae, apically bilinguate, laterally lacerate, ca. 1.5 mm. broad, basally cordate, the claw binute; stamens 5, 2–3 mm. long, the oblong anthers 0.5–0.8 mm. long; staminodia conspicuous, flap-shaped, 0.4 mm. high, 0.8 mm. broad; ovary at anthesis ovoid, the style slightly exceeding the anthers, trifid less than one-fourth of its length. Capsule subglobose, exceeding the sepals, 3.0–4.5 mm. long, 10–20-seeded, the seeds hippocrepiform, 1.0–1.5 mm. long, densely hispidulous dorsally, ventrally slightly umbonate, the facies merely puncticulate. Fig. 2A. (Holotype).

Known only from saline soils in the vicinity of Sierra del Rey and Laguna del Rey in Coahuila, Mexico.

The petals are completely unlike those of any other species and suggest the dorsal profile of a beetle. This peculiar aspect is approached, but only slightly, by the petals of the following species.

4. DRYMARIA SUBUMBELLATA I. M. Johnston, in Jour. Arn. Arb. 31:188. 1950. (HOLOTYPE: *I. M. Johnston 8489*, s. end of Cañada Oscuro near Tanque la Luz, confined to gypsum beds on the escarpment, western Coahuila; GH!)

Upright or ascending lignescent perennials to as much as 25 cm. high, the branches mostly opposite, the internodes longer or shorter than the leaves, glabrous or glaucescent, the taproot to 1 cm. thick. Leaves opposite or pseudoverticillate, the blades 1.5–4.0 cm. long, 0.5–1.0 mm. broad, glabrous or glaucescent, succulent, linear, apically obtuse, attenuate to the sessile base; true stipules absent. Inflorescences of terminal subumbelloid 3–9-flowered cymes, the peduncles 4–8 cm. long, the bracts mostly imbricate, lance-ovate, 2.5–4.0 mm. long; mature pedicels 3–7 mm. long, glabrous, the outer ones spreading. Sepals 5, 5–6 mm. long, 2–3 mm. broad, glabrous or bullate, broadly ovate, apically obtuse or acutish, the margins involute, the venation obscure, with 7–9 veins arising from the base, all but the midrib dichotomizing; petals 5, 4.5–6.0 mm. long, with 6–8 subequal apical laciniae, these lance-deltoid, attenuate, falcate, denticulate, the trunk longer than the laciniae, laterally lacerate, basally truncate to rounded, 1.0–2.0 mm. broad; stamens 5, 3.5–4.0 mm. long, the oblong anthers 0.8–1.0 mm. long; staminodia obsolescent; ovary at anthesis ovoid, the style slightly exceeding the anthers, bifid or trifid less than one-fourth its length, nearly as long as the ovary. Capsule subglobose, 5–6 mm. long, exceeding the sepals, 10–20-seeded, the seeds hippocrepiform, 1.2–1.5 mm. long, dorsally provided with dense white hairs to 0.5 mm. long, ventrally umbonulate, the facies smooth or puncticulate. Fig. 2B. (Holotype).

Known only from the type collection.

In the nature of the inflorescence and the petals, this bizarre species is intermediate between *D. elata* and the other two species in this homogeneous series.

5. Drymaria suffruticosa A. Gray ex S. Watson, in Proc. Am. Acad. 17:328. 1882. (holotype: *Palmer 74*; San Lorenzo de Laguna, Coahuila; GH!; isotypes at US, MO, UC, etc.!)

Upright suffrutescent glabrous perennials to as much as 30 cm. tall, the leaves often fascicled at the geniculate nodes, the taproot to as much as 8 mm. thick. Leaves pseudoverticillate, glabrous or glaucescent, somewhat succulent, linear, obtuse, 10–25 mm. long, ca. 1 mm. broad, basally tapering to the stem; stipules apparently lacking. Flowers globose in few-flowered terminal cymes, the peduncles and pedicels glabrous; bracts lanceolate, 3–5 mm. long, about equaling the pedicels. Sepals 5, 5–6 mm. long, 3–4 mm. broad, broadly ellipsoid, apically rounded but with a minute acumen, strongly venose throughout, the small scariose margins involute; petals 5, 4.5–5.5 mm. long, ca. 2 mm. broad, with 10–14 subequal apical laciniae, laterally lacerate, basally truncate or tapered to the minute claw; stamens 5, 4–5 mm. long, the oblong anthers ca. 1 mm. long; staminodia cupular, minute; ovary at anthesis renoid, the minute bifid style slightly exceeded by the anthers. Capsule broadly ellipsoid, ca. 6 mm. long, often capped by a stylopodium, many-seeded, the seeds hippocrepiform, ca. 0.9 mm. broad, dorsally provided with a row of stiff hairs to 0.5 mm. long. Fig. 2C. (Holotype).

Known only from the Coahuilan Desert of Mexico.

6. Drymaria lyropetala I. M. Johnston, in Journ. Arn. Arb. 21:68. 1940. (holotype: *I. M. Johnston 7594*; 3.5 km. s. of Cedral, gypsum plain, locally common, GH!)

Drymaria lyropetala var. *coahuilana* I. M. Johnston, in Jour. Arn. Arb. 31:189. 1950. (holotype: *R. N. Stewart 567* [cited as *Johnston 567* in original description]; 2 km. s. of Santa Elena, Sierra de las Cruces, Gypsum Ridge, Coahuila, GH!)

Upright or ascending glandular or glabrous perennials to as much as 30 cm. high, branching mostly at the base, the internodes shorter to longer than the leaves, apparently elongating belatedly, the taproot to 1 cm. thick. Leaves opposite or pseudoverticillate, 3–15 mm. long, 0.5–1.2 mm. broad, glabrous or glandular, glaucescent, succulent, linear, apically obtuse, attenuate to the sessile base, the upper leaves minutely stipulate. Inflorescences of terminal lax 3–9-flowered cymes, the peduncles 4–60 mm. long, glabrous to stipitate-glandular, the bracts 0.5–3.5 mm. long, remote, the mature pedicels 3–6 mm. long, glabrous or glandular, not recurved. Sepals 5, 3–5 mm. long, 1.5–3.0 mm. broad, glabrous to stipitate-glandular, ovate, apically obtuse, the venation obscure, with 7–9 veins arising from the base, all but the midrib dichotomizing; petals 5, 3.2–5.2 mm. long, with 10–12 unequal apical laciniae, these linear, obtuse, crenulate, the outermost as long as or longer than the trunk, the trunk laterally lacerate, basally cordate to truncate, 1–2 mm. broad; stamens 5, 3–6 mm. long, the oblong anthers 0.7–1.0 mm. long; staminodia cupular, to 0.4 mm. high; ovary at anthesis subcylindric, the style about as long, 1.5–2.5 mm. long, trifid about one-fourth its length; stylopodium well-developed. Capsule globose, 3.0–3.5 mm. long, 3–24-seeded, the seeds hippocrepiform, 1.0–1.5 mm. broad, ventrally umbonulate,

dorsally hispid, the hairs 0.2–0.3 (–0.5) mm. long, scanty and spreading. Fig. 1D. (Holotype of var. *lyropetala*); Fig. 1E (Holotype of var. *coahuilana*).

Local on gypsum soils of the Coahuilan Desert of Mexico.

The two varieties of this species may be separated by the following key:

a. Bracts 2–3.5 mm. long; leaves 5–15 mm. long, shorter than the internodes; plants glabrous to stipitate-glandular.....var. COAHUILANA

a. Bracts 0.5–1.5 mm. long; leaves 3–6 mm. long, shorter to longer than the internodes; plants glabrous or with a few sessile glands.....var. LYROPETALUM

Johnston erred very slightly in his description of the more southern var. *lyropetala*, stating that it was glabrous, the glandulosity occurring only in the northern variety. The type of var. *lyropetala* has a few scattered glands. It should be noted here that the UC isotype has leaves which are mostly longer than the internodes while the converse is true of the holotype, which incidentally is less conspicuously glandular.

C. Series STIPITATAE

7. DRYMARIA STIPITATA Fosberg, in Lloydia 4:281. 1941. (HOLOTYPE: *C. H. Muller 3301*; Mun. de Sierra Mojada, Sierra Mojada, Cañon de San Salvador; common in high oak chaparral; Coahuila; US!)

Upright suffrutescent perennials to as much as 20 cm. high, glabrous below, becoming stipitate-glandular above. Leaves opposite, the blades 5–15 mm. long, 1.5–5.5 mm. broad, glabrous, somewhat carnose, almost veinless, narrowly ovate to elliptic, apically acute, basally acutely tapering to the petiole, the petiole 1–2 mm. long; stipules apparently lacking. Inflorescences of few-flowered terminal cymes, the axes glandular-puberulent, locally densely so; bracts lance-ovate, 1.5–2.5 mm. long, apically acuminate; pedicels mostly 3–5 mm. long. Sepals 5, subequal, lanceolate to ovate, apically acuminate, basally umbonate, 5–6 mm. long, 1.5–2.5 mm. broad, transparent save for the 3 ribs; petals 5, 5.0–5.5 mm. long, apically and laterally lacerate, the laciniae linear, often dichotomous, some of the lateral laciniae directed downwardly; stamens 5, 5.0–5.5 mm. long, the broadly oblong anthers ca. 0.8 mm. long, alternating with 5 clavate staminodia to as much as 2.2 mm. long; ovary at anthesis ellipsoid, much shorter than the style, the style trifid for ca. one-fifth its length, exceeding the anthers. Capsule ca. 4 mm. long, 6–8-seeded, the seeds 0.8–1.0 mm. long, symmetrically hippocrepiform, the surfaces irregularly corrugated. Fig. 3A (Holotype).

Coahuila, Tamaulipas and probably Nuevo Leon, Mexico.

D. Series ARENARIOIDES

Leaves linear to narrowly ovate, opposite or pseudoverticillate, subsessile, stipulate. Flowers in cymes, racemes or solitary in the axils of slightly reduced foliage leaves. Sepals mostly obtuse and weakly nerved. Petals 2–8-lobed, the trunk much longer than the claw, entire or denticulate. Seeds hippocrepiform and dorsally sulcate or lacrimiform, nearly smooth or granular. Five species in western U. S., northern Mexico and Baja California. Figs. 3B, 3C, 4.

a. Leaves linear, pseudoverticillate, glabrous; flowers cymose, the bracts clearly different from the foliage leaves.....8. D. MOLLUGINEA

a. Leaves linear to ovate, opposite or pseudoverticillate; glabrous to densely stipitate-glandular; inflorescences tending to be racemose, the bracts often not different from foliage leaves.

b. Plants stipitate-glandular; flowers in the axils of scarcely reduced foliage leaves or racemose:

c. Flowers racemose, the petals mostly 4–6 lobed; leaves linear to oblong:

d. Petals 4.0–6.2 mm. long, mostly 6-lobed, the middle lobes nearly as long as the outer; sepals 4–7 mm. long; styles 1.0–2.5 mm. long, united more than half their length; continental Mexico.....9a. D. ARENARIOIDES ssp. ARENARIOIDES

d. Petals 2.8–4.0 mm. long, 2–6-lobed, the middle lobes about half as long as the outer; sepals 2.8–4.0 mm. long; styles 2.8–4.5 mm. long, united half their length or less. Baja California.....9b. D. ARENARIOIDES ssp. PENINSULARIS

c. Flowers axillary, the petals merely bifid; leaves ovate.....10. D. AXILLARIS

b. Plants without stipitate glands; flowers in cymes:

e. Leaves linear to oblong; petals occasionally trifid, briefly unguiculate; seeds brownish, tuberculate.....11. D. BARKLEYI

e. Leaves elliptic to ovate; petals bifid, exunguiculate; seeds yellowish, nearly smooth.....12. D. POLYCARPOIDES

8. DRYMARIA MOLLUGINEA (Lag.) Didr. in Linnaea 29:738. 1859. (HOLOTYPE: "*Lagasca 1806*" annotated by De Candolle in the De Candolle Herbarium; G. *n. v.*; photograph and drawing of type at GH!)

Alsine molluginea Lag. Gen. & Sp. 13. 1815.
Arenaria ? molluginea Ser. ex DC. Prodr. 1:400. 1824.
Drymaria sperguloides A. Gray, Pl. Fendler 11. 1849. (HOLOTYPE: *Fendler 55*; New Mexico, GH!; isotypes at US, UC, F, Mo, etc.)
Lepigonum molluginea Fries, Ind. Hort. Sem. 1856.
Mollugophytum sperguloides (A. Gray) M. E. Jones, Extr. Contr. West. Bot. 18:35. 1933.

Slender erect virgate or dichotomously branched annuals to as much as 20 cm. high, the internodes shorter to longer than the leaves, glabrous or with sessile glands, the tap root ca. 1 mm. thick. Leaves mostly pseudoverticillate, glabrous or scantily glandular, 9–25 mm. long, 0.5–2.0 mm. broad, linear, apically obtuse, attenuate to the sessile base, the stipules lance-deltoid, 1–2 mm. long. Inflorescences of terminal cymose racemes, only the first 1 or 2 branches cymose, subsequent branching tending to be racemose, the peduncle 8–30 mm. long; bracts 1.0–2.5 mm. long, the pedicels 2–5 mm. long, glabrous to minutely stipitate-glandular. Sepals 5, 2.5–3.5 mm. long, glabrous or minutely glandular, oblong, apically obtuse and often cucullate, only the midrib prominent; petals 5, 1.7–2.5 mm. long, 0.4–0.7 mm. broad, apically provided with usually 4 lacinae, the outer one-third to one-half as long as the trunk, the inner occasionally absent or reduced to mere dentations, the trunk subdeltoid, laterally denticulate, truncate or tapered to the minute claw; stamens 5, 1.5–2.0 mm. long, the oblong to suborbicular anthers 0.4–0.5 mm. long; staminodia absent; ovary at anthesis globose, ca. 2 mm. long, the style 2–3-cleft nearly to the base, less than 1 mm. long; stylopodium absent. Capsule subglobose, 2–3 mm. long, exceeding the sepals, 3–17-seeded, the seeds 0.9–1.4 mm. broad, dark brown or purplish in age, hippocrepiform, dorsally flat, scarcely umbonate ventrally, minutely corrugated or tuberculate, the tubercles broader than long. Fig. 3B (Holotype of *D. sperguloides*); Fig. 3C ("*D. molluginea* Fenzl" at LE).

Sandy soils, Arizona to western Texas, U. S. A.; south to Puebla, Mexico.

The specimen from Leningrad (Fig. 3C) apparently from the Ledebour herbarium, and labeled "*Drymaria molluginea* Fenzl" lacks the inner laciniae of the petals. I doubt that this feature has any taxonomic significance. A close parallel is exhibited by *D. arenarioides* ssp. *peninsularis* where the form which lacks the two central laciniae has been described as *D. johnstonii.* In both *D. molluginea* and *D. arenarioides* ssp. *peninsularis* specimens have been examined in which 1 or 2 of many flowers dissected had the inner laciniae reduced to mere dentations or apparently completely lacking.

Fig. 3: A. *D. stipitata* (holotype); habit, ½×; petal, 6×; sepal, 6×; stamen, 6×; staminode, 6×; seed, 10×. B. *D. molluginea* (holotype of *D. sperguloides*); petal, 12½×, seed, 15×; sepal, 12½×. C. *D. molluginea* ("D. molluginea Fenzl." at LE); habit, ½×.

9a. DRYMARIA ARENARIOIDES ssp. ARENARIOIDES

Drymaria arenarioides Humb. & Bonpl. ex Roem. & Schult. Syst. Veg. 5:406. 1819. (HOLOTYPE: *Humb. & Bonpl. 4070* ad Pachuca, probably destroyed at Berlin; isotype at P!)
Drymaria frankenioides HBK. Nov. Gen. & Sp. 6:21. *pl. 515.* 1823.

Prostrate radially spreading herbaceous or lignescent perennials to as much as 20 cm. long, branching mostly at the base, the internodes shorter to longer than the leaves, stipitate-glandular, the taproot to as much as 5 mm. thick. Leaves opposite or pseudoverticillate, stipitate-glandular, the blades linear-oblong to narrowly elliptic, apically obtuse, obscurely 1-nerved, 5–15 mm. long, 1–3 mm. broad, basally tapered to the petiole, the petiole ca. 1 mm. long; stipules lance-deltoid, 1.0–2.5 mm. long, entire. Flowers, except the first formed, solitary in the axils of slightly and gradually reduced foliage leaves, the mature pedicels 3–15 mm. long, stipitate-glandular, the subtending leaves stipulate. Sepals 5, 4–7 mm. long, 1–3 mm. broad, stipitate-glandular, oblong to broadly elliptic, the venation obscure, subdendritic, the inner sepals shorter, broader and less glandular; petals 5, 4.0–6.5 mm. long, apically (4–) 6–8-lobate, the outer lobes slightly longer and broader, about as long as the trunk, the inner lobes linear, equal, the trunk laterally denticulate, 0.8–1.5 mm. broad; stamens 5, ultimately 3–5 mm. long, the oblong anthers 0.8–1.2 mm. long; ovary at anthesis ellipsoid, the style bifid or trifid less than half its length, slightly exceeding the stamens; stylopodium often conspicuous. Capsule ovoid, 3–5 mm. long, 15–25-seeded, the seeds hippocrepiform, dorsally flattened or sulcate, exumbonate, minutely tuberculate, 0.8–1.2 mm. broad. Fig. 4A.

Sonora, Chihuahua, Zacatecas, San Luis Potosi, Guanajuato and Hidalgo, Mexico, usually in sandy soils.

It would appear that Humboldt and Bonpland or Kunth had some reason for changing the name *D. arenarioides* to *D. frankenioides* as Roemer and Schultes cited the name as follows: "D. arenarioides Humb. et Bonpl. . . . Reliqu. Willd. MS". I would judge that Willdenow had written the name "D. arenarioides Humb. & Bonpl." on his herbarium specimen and that Roemer and Schultes were the first to publish the name, probably furnished earlier by Humboldt and Bonpland. Two other names in *Drymaria* seem to have the same history, i.e. *D. ovata* and *D. stellarioides*. The question then arises whether the name should bear the authority "Humb. & Bonpl. in Roem. & Schult.", "Humb. & Bonpl.: Willd. ex Roem. & Schult." or "Willd. ex Roem. & Schult." Most publications appear to make use of the latter, but I feel it more proper to credit the name to Humboldt and Bonpland as did Willdenow in his herbarium. At any rate, *D. arenarioides* and *D. frankenioides* are names based on the same specimen (typonyms).

In its diminished leaves, sepals and petals, *Parry & Palmer 49* from San Luis Potosi, approaches *D. arenarioides* subsp. *peninsularis*, but the petals, which seem to possess more constant characters, are like those of typical *arenarioides*, i.e. two larger outer lobes and two basally dichotomous inner lobes, the linear divisions of the inner lobes being nearly as long as the oblong outer lobes. The very long style of this specimen further corroborates its determination as *D. arenarioides* ssp. *arenarioides*.

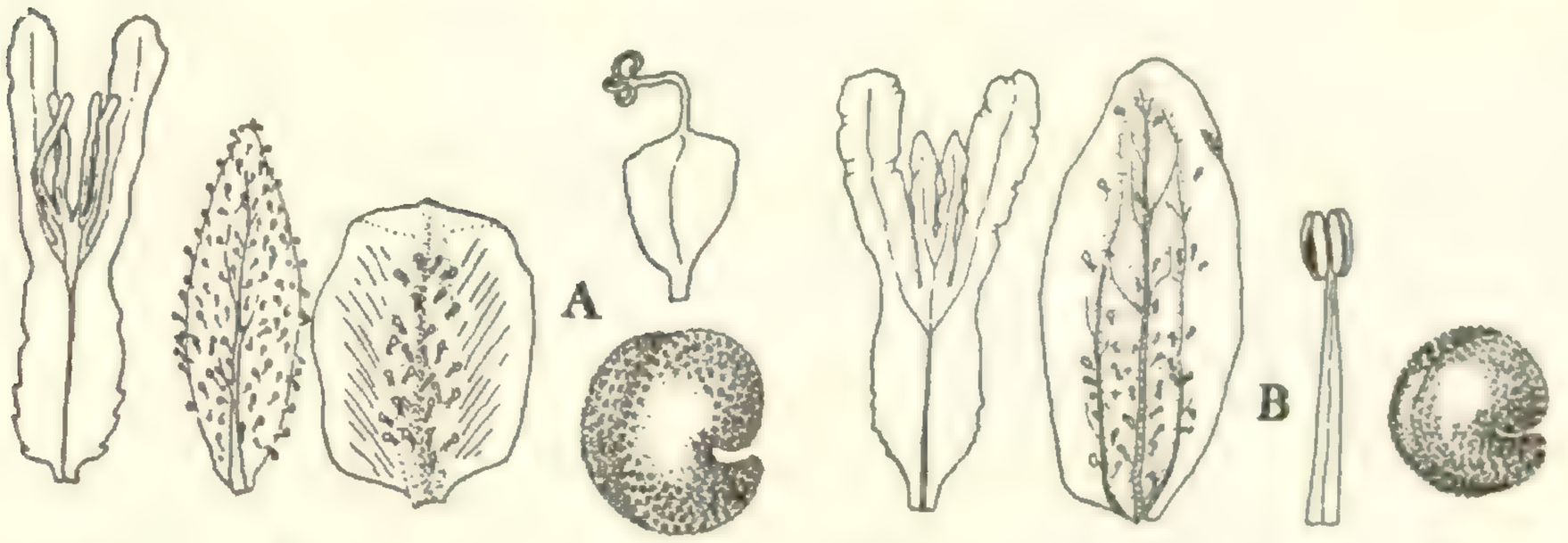

Fig. 4: A. *D. arenarioides* ssp. *arenarioides*; petal, 10×; outer sepal, 10×; inner sepal, 10×; gynoecium, 6×; seed, 15×. B. *D. arenarioides* ssp. *peninsularis* (holotype); petal, 10×; sepal, 10×; stamen, 10×; seed 12½×. C. *D. axillaris* (isotype); petal, 5×; sepal, 5×; stamen, 5×; seed, 15×. D. *D. arenarioides* ssp. *peninsularis* (holotype of *D. johnstonii*); petal, 10×; sepal 10×; seed, 20×. E. *D. barkleyi* (holotype, except seed); petal, 10×; sepal, 10×; seed, 20×; habit, ½×. F. *D. polycarpoides* (holotype, except seed); petal, 10×; sepal, 10×; seed, 20×.

9b. DRYMARIA ARENARIOIDES ssp. **peninsularis** (S. F. Blake) J. Duke comb. & stat. nov.

Drymaria peninsularis S. F. Blake, in Jour. Wash. Acad. 14:285. 1924. (HOLOTYPE: *Purpus 423*; Cape Region, Baja California, US!; isotypes at UC, F, GH, MO)
Drymaria johnstonii Wiggins, in Proc. Cal. Acad. 4^{25}:203. 1944. (HOLOTYPE: *I. M. Johnston 3972*; in crevices of rock on mesa near crest of island, the isthmus, Espiritu Santo Island, Baja California, CAS!)

Radially spreading or ascending annuals or suffrutescent perennials to as much as 25 cm. long, branching mostly at the base, the internodes shorter to longer than the leaves, stipitate-glandular, the taproot to as much as 1 cm. thick. Leaves opposite or pseudoverticillate, stipitate-glandular, linear, obtuse, obscurely veined, 4–25 mm. long, 0.5–1.0 mm. broad, attenuate to the sessile base, the stipules lance-deltoid, entire, 0.5–1.5 mm. long. Flowers, except the first formed, solitary in the axils of slightly and gradually reduced foliage leaves, the mature pedicels 4–12 mm. long, stipitate-glandular, the subtending leaves stipulate. Sepals 5, 2.8–4.5 mm. long, 1.0–2.2 mm. broad, stipitate-glandular, oblong to broadly elliptic, obtuse, the venation obscure, subdendritic, the inner sepals shorter, broader and less glandular; petals 5, 2.8–4.0 mm. long, apically 4(–8)-lobate, the outer lobes longer, about as long as the trunk, the inner about half as long as the outer, the trunk laterally denticulate, basally truncate or tapered to the minute claw; stamens 5, ultimately 2–3 mm. long, the oblong anthers 0.5–0.8 mm. long; ovary at anthesis obovoid, stipitate, the minute style slightly exceeded by the anthers. Capsule globose, 2.5–4.0 mm. long, the style less than 1 mm. long, trifid about half its length, the seeds 10–20, hippocrepiform, dorsally flattened or sulcate, scarcely umbonate ventrally, reticulate or minutely tuberculate, 0.6–1.0 mm. long. Fig 4B (Holotype of *D. peninsularis*); Fig. 4D (Holotype of *D. johnstonii*).

Sandy soils; Cape Region of Baja California, Mexico.

Unquestionably this subspecies is intimately related to ssp. *arenarioides*. The two subspecies are nicely separated by the Gulf of California in addition to the diagnostic characters listed in the key. I have seen many specimens of both subspecies, and intermediates are few indeed. *Craig 738* and *Howell 10576* appear to represent intermediates with many of the petals similar to those of the typical subspecies. Other features, coupled with the geography, seem to justify their relegation to ssp. *peninsularis*.

10. DRYMARIA AXILLARIS Brandegee, in Univ. Cal. Publ. Bot. 4:178. 1911. (HOLOTYPE: *Purpus 4526*; Sierra del Rey, Coahuila, UC!; isotypes at GH, US, F, MO, etc.)

Upright glandular-pubescent, cyanic glaucous perennials to 10 cm. high with many suffrutescent branches arising near the base, the taproot to 6 mm. in diameter. Leaves opposite, cyanic, glaucous, densely glandular-pubescent with capitate hairs to 0.7 mm. long, broadly ellipsoid, apically obtuse to acutish, basally subcordate or tapered to the petiole, 3–12 mm. long, 2.5–8.0 mm. broad; veins not apparent; petioles 0.5–2.0 mm. long, the stipules entire, broadly deltoid, 0.5–1.0 mm. long. Flowers solitary in the axils of reduced leaves, the glandular-pubescent pedicels

ebracteate, 1.5–3.0 mm. long. Sepals 5, subequal, subsucculent, glandular-pubescent, broadly lanceolate to ovate, slightly concavo-convex, obtuse to acutish, 4–5 mm. long, 1.5–2.0 mm. broad; venation obscure, the margins scariose; petals 5, 3.5–4.0 mm. long, bifid about half their length, the lobes obtuse, ca. 0.6 mm. broad, exappendiculate, the claw 0.5–1.0 mm. broad; stamens 5, 3.0–3.5 mm. long, the oblong anthers ca. 0.8 mm. long; ovary at anthesis broadly ellipsoid, the style bifid about one-third its length, slightly exceeding the anthers. Capsule bivalved, ca. 2.5 mm. long, many-seeded, the seeds hippocrepiform, merely reticulate or puncticulate, ca. 0.7 mm. broad. Fig. 4C (Isotype).

Known only from the type locality in Coahuila, Mexico.

11. Drymaria **barkleyi** J. Duke and Steyermark sp. nov.

Plantae annuae graciles ramis paucis internodis glaucis quam foliis longioribus radice non viso. Folia opposita laminis glabris glaucis bullatisque 4–10 mm. longis, 1.0–2.5 mm. latis, ellipticis apice obtusis subsessilibus stipulis minutis deltoideis caducis apice saepe bifidis. Flores solitarii in axillis foliorum vix reductorum pedicellis glabris 4–8 mm. longis. Sepala (4–) 5, 3.0–4.5 mm. longa ca. 1 mm. lata glabra oblongo-elliptica obscuriter venosa; petala 5, 2.5–3.5 mm. longa ultra medium bifida vel rariter trifida lobis oblongis obtusis emarginatisve denticulatis basi acutis unguibus minutis; stamina (4–) 5, 3 mm. longa antheris oblongis 0.8–1.0 mm. longis; ovarium oblongum, 1–2 mm. longum saepe 10-ovulatum stylis ca. 1.5 mm. longis (3-) 4-lobis minutis. Capsulae non visae. Fig. 4E (Holotype [except seed]).

Coahuila: low pointed hill, almost destitute of soil, apparently a limestone shale, 25 mi. sw. of Monterrey, *Warnock & Barkley 148 26 M.* (holotype: F, isotype at US).

Fortunately another specimen with mature capsules is referable to the new species. *Hernandez, Rowell & Barkley 16M531*, collected on talc-like limy soil and shaly limestone, (in Nuevo Leon), 11 mi. w. of Santa Catarina differs only in having a few sessile glands on the herbage. The capsule is yellow, 3–4-toothed, 2.5–3.0 mm. long, 4–8 seeded. The seeds are lacrimiform, ca. 0.7 mm. in diameter, minutely and remotely tuberculate. Apparently the closest related species is the preceding with which the new species shares the cyanic tinting, solitary axillary flowers, and minute deltoid stipules. The differences far outnumber the strictly superficial similarities however. The sharply pointed long-beaked seed is slightly reminiscent of *D. debilis*.

12. Drymaria polycarpoides A. Gray, Pl. Fendl. 12. 1849. (holotype: *Gregg s. n.*; valley of Bolsón de Mapimí, Mexico; GH!)

Prostrate or ascending profusely branching perennials to as much as 10 cm. long, branching mostly from the base, the nodes geniculate, fragile, the internodes mostly shorter than the leaves, glabrous or quite glaucous, the taproot to as much as 1 cm. thick. Leaves opposite, carnose, glaucous, often cyanic, elliptic, apically acute to obtuse, basally tapered, 5–12 mm. long, 2–5 mm. broad, weakly if at all nerved; petioles 0.5–1.5 mm. long, exceeding the minute, entire, lance-deltoid

stipules. Flowers in few-flowered strongly dichotomous cymes, the pedicels 1–4 mm. long, the bracts deltoid, obtuse, not scariose, 0.8–1.5 mm. long. Sepals 5, 3.5–5.0 mm. long, 1.5–2.0 mm. broad, glaucous, oblong to ovate, apically obtuse and often cucullate, the scariose margin as broad as or broader than the central 3-nerved portion; petals 5, 3.5–4.5 mm. long, bifid little more than half their length, the lobes broadly oblong, apically obtuse, 1–3-nerved, merging imperceptibly with the trunk, the trunk 1.0–1.5 mm. long, nearly as broad, exunguiculate or subexunguiculate; stamens 5, the anthers 0.8–1.0 mm. long, the filaments 1.5–2.5 mm. long, devoid of staminodia; ovary at anthesis ovoid, equaled or exceeded by the style, the style trifid for less than one-fourth its length. Capsule ellipsoid to oblongoid, 2.0–2.5 mm. long, few-seeded, the seeds lacrimiform, not circinate, umbonulate ventrally, smooth, yellowish-brown. Fig. 4F (Holotype [except seed]).

Known only from the Coahuilan Desert of Mexico.

E. Series VISCOSAE

13. DRYMARIA VISCOSA S. Watson ex Orcutt, in West. Am. Sci. 2:57. 1886. *nomen nudum*. S. Watson in Proc. Am. Acad. 22:469. 1887. (HOLOTYPE: *Orcutt 1330*, Socorro ("Socono"), n. Baja California, GH!; isotypes at UC, D, F, US, MO, NY, etc.)

Prostrate radially spreading or ascending diffusely branched viscid annuals, the branching below the inflorescence mostly dichotomous, the taproot to as much as 5 mm. thick. Leaves pseudoverticillate or opposite, glandular-puberulent, linear, apically obtuse, basally tapering to the clasping petiole, 3–15 mm. long, 0.5–1.5 mm. broad, the petiole 1–3 mm. long; stipules acicular, caducous, 1.0–1.5 mm. long. Flowers campanulate in 1–5-flowered cymes, the peduncles mostly glabrous; bracts deltoid, marginally ciliolate, 0.5–1.0 mm. long, the pedicels 0–3 mm. long, all but the central equaled or exceeded by the bracts. Sepals 5, 2.3–3.0 mm. long, 1–1.5 mm. broad, glandular-puberulent, oblong, obtuse, obscurely 3-nerved, the midrib subapically excurrent; petals 5, 1.8–2.2 mm. long, bifid about two-thirds their length, the lobes oblong, obtuse, tapered to the unguiculate base, exappendiculate; stamens 5, ca. 2 mm. long, the broadly oblong anthers ca. 0.4 mm. long; ovary at anthesis ellipsoid, about equaled by the style, the style trifid about half its length, barely exceeding the anthers. Capsule 2.0–2.5 mm. long, equaling or exceeded by the sepals, 5–15-seeded, the seeds cochleate, nearly smooth, 0.5–0.6 mm. broad, dorsally brown, facially transparent and colorless, the yellowish embryo visible. Fig. 5A (Isotype).

Sandy soils of Baja California, Mexico.

In habit, this plant is not unlike *D. molluginea* as pictured in Fig. 3D.

F. Series ORTEGIOIDES

14. DRYMARIA ORTEGIOIDES Griseb. Cat. Pl. Cub. 21. 1866. (HOLOTYPE: *Wright 2019*; Cuba occ., GOET!; isotypes at F, GH, MO, US, etc.)

Pinosia ortegioides (Griseb.) Urban, in Ark. Bot. 23A5:71. 1930.

Upright sparsely dichotomizing glabrous or glandular perennials to as much as 20 cm. high, the internodes much longer than the leaves, the tap root to 5 mm. thick. Leaves opposite, glabrous, linear to elliptic, apically acute to obtuse, attenuate to the subsessile base, 3–12 mm. long, 1.0–3.5 mm. broad, the stipules lance-deltoid, 0.3–0.8 mm. long, entire. Inflorescences of terminal condensed 5–21-flowered dichotomous cymes; peduncles 1.5–3.5 cm. long, the bracts 1–2 mm. long, imbricate or subimbricate, the glabrous pedicels 1.5–4.0 mm. long. Sepals 5, 2.5–3.5 mm. long, glabrous, ovate to obovate, acute to obtuse, the venation obscure, dichotomous and reticulate; petals 3, 2.3–3.2 mm. long, twice dichotomous, the lobes oblong, obtuse, nearly as long as the trunk, exappendiculate, the trunk merging gradually with the claw; stamens 3, the oblong anthers ca. 0.5 mm. long; ovary subglobose, the styles 0.5–1 mm. long. Capsule globose, 1.5–2.0 mm. long, shorter than the sepals, 1–4-seeded, the seeds hippocrepiform, scarcely if at all umbonulate, closely tuberculate, 1.0–1.5 mm. long, dark brown. Fig. 5B, 5C.

Sandy savannas of Cuba.

G. Series EXCISAE

Leaves deltoid-ovate to reniform, opposite, stipulate. Flowers long-pedicellate in lax cymes. Sepals acute or obtuse, trinerved. Petals bifid, the lobes themselves dichotomizing, ciliate-auriculate at their bases. Seeds cochleate, tuberculate, the tubercles domical or substellate. 3 species in Mexico. Fig 5 D–F.

a. Plants merely glandular-puberulent to glabrous; leaves deltoid-ovate to reniform, rounded to acute at the base; petals apically 2–4-times dichotomous.
  b. Leaves deltoid-ovate; sepals and petals ca. 5 mm. long, the petals 4 times dichotomous. ..... 15 D. HYPERICIFOLIA
  b. Leaves orbicular to cordate or reniform; sepals 5.0–10.0 mm. long; petals 6–12 mm. long, 2–3 times dichotomous..... 16. D. EXCISA
a. Plants stipitate-glandular to villose; leaves ovate to reniform, subcordate at the base; petals 1–2-times dichotomous, if only once dichotomous, the veins and usually the apex giving evidence of the second dichotomy..... 17. D. LONGEPEDUNCULATA

15. DRYMARIA HYPERICIFOLIA Briq. in Ann. Cons. & Jard. Geneva 14:369. 1911. (HOLOTYPE: *Jurgenson 38*, de Lecambre de Yolotepeque à Juquilla, au sud-ouest d'Oaxaca; Mexicum G!; isotype at K)

Erect or ascending perennials (?) to as much as 25 cm. high, the internodes about as long as the leaves, stipitate-glandular. Leaves opposite, 8–22 mm. long, 5–14 mm. broad, narrowly deltoid-ovate, glabrous or minutely glandular-puberulent below, apically acute, marginally somewhat undulate, basally obtuse to acute, plinerved; petioles 1–2 mm. long, the stipules entire or bifid, the divisions lance-deltoid, 0.5–1.2 mm. long. Inflorescences of terminal 5–11-flowered cymes, the peduncles 2–3 cm. long, the bracts lanceolate, 1.5–2.5 mm. long, the pedicels stipitate-glandular, 4–6 mm. long. Sepals 5, 4.5–5.5 mm. long, lanceolate to narrowly ovate, apically acute, the outer sepals scantily stipitate-glandular, trinerved; petals 5, ca. 6 mm. long, four times dichotomous, the ultimate segments emarginate, the trunk laterally provided with deciduous ciliate auricles; stamens 5, ca. 4 mm. long, the anthers oblong, ca. 0.7 mm. long; ovary at anthesis ellipsoid, about equaled by the partially trifid style, the style slightly exceeded by the anthers.

Capsule ellipsoid, ca. 5 mm. long, 3-valved, apically constricted, many-seeded, the seeds cochleate, 0.7–1.0 mm. long, irregularly corrugated or tuberculate; seeds immature. Fig. 5D (Holotype).

Known only from two collections near Juquila in Oaxaca, Mexico.

North American authors have confused *Drymaria ladewii* with this species, probably because of certain vegetative resemblances. The flowers of the two species however contrast vividly.

16. Drymaria excisa Standl. in Field Mus. Bot. 8:11. 1930. (holotype: *Mexia 1748*; Real Alto, trail to El Tajo de Santiago, 2500 m., Jalisco, F!; isotypes at UC, GH, etc.)

Drymaria grandis Bullock, in Kew Bull. 1936:389. 1936. (holotype: *Hinton 5427*, Los Hornos, Temascaltepec, 2500 m., Mexico, K!; isotypes at GH, MO, etc.)

Robust spreading perennials, the procumbent or erect branches to 3 m. long (fide Bullock), the internodes mostly longer than the leaves, glandular-puberulent, glabrescent. Leaves opposite, 5–25 mm. long, 5–30 mm. broad, glabrous or minutely glandular, the blades orbicular to obcordate, apically emarginate or apiculate, marginally entire, basally obtuse to truncate, 3-pli-nerved; petioles 5–25 mm. long, the stipules entire or apically lacerate, lanceolate, 2–4 mm. long. Inflorescences of terminal lax 3–many-flowered cymes, the peduncles 3–6 (–15) cm. long; bracts lanceolate to ovate, 3.0–4.5 mm. long, the pedicels 3–15 mm. long, stipitate-glandular, glabrescent. Sepals 5, 5.0–10.0 mm. long, 2.0–2.8 mm. broad, ovate, apically acute, weakly 3-ribbed; petals 5, 6–12 mm. long, 2–3-times dichotomous, the ultimate segments entire or emarginate, the trunk laterally provided with several deciduous ciliate auricles; stamens 5, 5.0–6.5 mm. long, the oblong anthers ca. 1 mm. long, the staminodia minute, semicircular; ovary at anthesis ovoid, about equaling the style, the style 1.5–3.0 mm. long, trifid about one-third its length. Capsule ellipsoid, apically constricted, 3.0–5.5 mm. long, many-seeded, the seeds tightly cochleate, 0.9–1.2 mm. broad, evenly tuberculate, the dorsal tubercles somewhat longer than broad, the facial tubercles polygonal (rarely substellate) in outline. Fig 5E (Holotype).

Jalisco, Michoacan, Mexico, and Morelos, Mexico, usually above 2000 m.

It is interesting to note that in none of the original descriptions of taxa referable to this species (or series) was any mention made of the polydichotomous nature of the petals. This may be due to the fact that the foliage is so outstanding that the species can usually be determined without resorting to the tedium of dissection.

17. Drymaria longepedunculata S. Watson, in Proc. Am. Acad. 25:142. 1890. (holotype: *Pringle 2121*; under ledge of the barranca near Guadalajara, GH!; isotypes at UC, US, etc.)

Laxly spreading or rarely erect annuals, the internodes mostly longer than the leaves, villose with spreading jointed hairs or stipitate-glandular. Leaves opposite, 5–14 mm. long, 5–20 mm. broad, villose to glabrous, reniform to deltoid-ovate, apically rounded to acute and apiculate, marginally entire, basally truncate or

Fig. 5: A. *D. viscosa* (isotype); petal, 10×; sepal, 10×; stamen, 10×; seed, 15×. B. and C. *D. ortegioides;* petal, stamen, outer and inner sepals, all 10× (from holotype); seed, 10×; habit, ½×. D. *D. hypericifolia* (holotype); petal, 10×; sepal, 5×; seed, 20×. E. *D. excisa* (holotype); petal, 4×; sepal, 4×; stamen, 4×; seed, 10×. F. *D. longepedunculata* (holotype); habit, ½×; petal, 5×; sepal, 5×.

cordate, 3–7–pli-nerved; petioles 1–6 mm. long, stipules entire or bifid, the divisions filiform to narrowly lanceolate, 1.0–1.5 mm. long. Inflorescences of lax terminal 3–many-flowered cymes, the peduncles 1–10 cm. long; bracts lanceolate, 1.5–2.5 mm. long, the pedicels 5–25 mm. long, sparingly villose with glandular hairs occasionally admixed. Sepals 5, 4.2–5.5 mm. long, 1.7–2.7 mm. wide, glabrous to villose, narrowly to broadly ovate, the outer acute, villose, and weakly 3-nerved, the inner rounded and glabrous; petals 5, 5.6–7.0 mm. long, once or twice dichotomous, the ultimate segments emarginate, the trunk laterally provided with several ciliate auricles; stamens 5, 4–5 mm. long, the oblong anthers 0.8–1.0 mm. long; ovary at anthesis subglobose, 1–2 mm. long, the style 2.0–2.5 mm. long, trifid about one-third its length, exceeded by the anthers. Capsule 3.5–5.0 mm. long, many-seeded, the seeds 0.7–0.9 mm. long, cochleate, evenly tuberculate, the dorsal tubercles conical, the facial tubercles elongate-stellate. Fig. 5F (Holotype).

Jalisco, Michoacan, and Mexico, Mexico.

Here the tendency toward a second dichotomy in the petals is often suppressed to the point that the petal is merely bilobed, but the lobes are emarginate, and the twice-dichotomous nature is still reflected in the venation. This species affords a good transition to the series VILLOSAE. *McVaugh & Koelz 897* from Jalisco makes a marked approach toward *D. multiflora,* and may represent a hybrid. Indicative of hybrid tendencies are the broadly reniform leaves, the absence of villosity, and the weakly emarginate petals. The floral parts in general are a bit small for *D. longepedunculata* and come closer to the range of dimension exhibited by the flowers of *D. multiflora.*

H. Series LEPTOPHYLLA

Leaves linear, oblong or narrowly spatulate, subsessile, stipulate, the stipules usually entire. Flowers in bracteate cymes, the pedicels longer or shorter than the bracts. Sepals obtuse to acuminate, trinerved. Petals bilobed, unguiculate, exauriculate, the lobes 1(–3)-nerved. Seeds cochleate, tuberculate, the tubercles not ornate. Two polymorphic intergrading delicate annual (or rarely perennial) species; western U. S. A. to Guatemala. Fig. 6.

a. All the sepals obtuse, often cucullate; seeds laxly cochleate, the anterior end not strongly recoiled:

  b. Plants usually taller than 5 cm., subvirgate, branching above the base; bracts mostly equaled or exceeded by the subtended pedicels; lobes of the petals 1–3-nerved.

    c. Peduncles and pedicels stipitate-glandular; lobes of the petals oblong, 1-nerved.....18a. D. EFFUSA var. EFFUSA

    c. Peduncles and pedicels glabrous or with sessile glands; lobes of the petals obovate, mostly trinerved.....18b. D. EFFUSA var. CONFUSA

  b. Plants minute, mostly less than 5 cm. tall; branching mostly from the base and in the inflorescence; bracts mostly exceeding the subtended pedicels; lobes of the petals 1-nerved.....18c. D. EFFUSA var. DEPRESSA

a. Some or all of the sepals acute to acuminate; seeds tightly cochleate, the anterior end strongly recoiled.

  d. Peduncles, pedicels and sepals devoid of stipitate-glands, the pedicels mostly shorter than the subtending bracts; petals bifid half their length or less, shorter than the sepals.....19a. D. LEPTOPHYLLA var. LEPTOPHYLLA

d. Peduncles and often the pedicels and sepals stipitate-glandular, the pedicels mostly longer than the subtending bracts; petals bifid for more than half their length, included by or exerted from the calyx:

e. Sepals lanceolate, exceeding the petals, not stipitate-glandular; plants subsuffrutescent. .....19b. D. LEPTOPHYLLA var. COGNATA

e. Sepals ovate, equaled or exceeded by the petals, usually stipitate-glandular; plants not suffrutescent.....19c. D. LEPTOPHYLLA var. NODOSA

18a. DRYMARIA EFFUSA var. EFFUSA

Drymaria effusa A. Gray, Pl. Wright. 2:19. 1853. (HOLOTYPE: *Wright 869*, mountains east of Santa Cruz, Sonora, GH!)

Erect, delicate, sparsely branched annuals to as much as 25 cm. high, the internodes mostly longer than the leaves, minutely glandular-puberulent or glabrate, the roots to ca. 1 mm. thick. Basal leaves pseudoverticillate, spatulate to orbicular; cauline leaves opposite, rarely pseudoverticillate, 5–25 mm. long, 0.5–1.2 mm. broad, minutely puberulent or glabrous, linear, apically obtuse or apiculate, sessile, the stipules entire, acicular, caducous, 0.5–1.0 mm. long. Inflorescences of terminal multifloriferous cymes, the ultimate branches showing tendencies to become monopodial; peduncles 2–5 cm. long, stipitate-glandular; bracts ovate, 0.5–1.8 mm. long, the mature pedicels 1–5 mm. long, stipitate-glandular, usually exceeding the bracts. Sepals 5, 1.4–2.2 mm. long, the outer narrower, shorter, more obtuse and often cucullate, glandular, the inner more ovate, often acutish, all trinerved, the veins subapically confluent; petals 5, 2–4 mm. long, bifid half their length or more, the lobes linear to oblong, 1-nerved, obtuse, tapering gradually to the claw, exappendiculate; stamens 5, 1.2–1.6 mm. long, the oblong anthers ca. 0.3 mm. long; ovary at anthesis ellipsoid, the style rather elongate, trifid about half its length, about attaining the anthers. Capsule ellipsoid, nearly equaling the sepals, the stigmata exerted; seeds 2–9, cochleate to lacrimiform, coarsely tuberculate, 0.5–0.8 mm. broad. Fig. 6B (Holotype).

Arizona, U.S.A.; Sonora and Sinaloa, Mexico, the Sinaloa specimens approaching *D. leptophylla.*

18b. DRYMARIA EFFUSA var. **confusa** (J. N. Rose) J. Duke comb. & stat. nov.

Drymaria confusa J. N. Rose, in Contr. U. S. Nat. Herb. 5:133. 1897. (HOLOTYPE: *Palmer 59*, southwestern Chihuahua, US!, isotypes at GH, MO, etc.)

Delicate sparsely branching glabrous or subglabrous annuals to as much as 7.5 cm. high, scarcely branching at the base. Basal leaves glabrous, orbicular to broadly elliptic, 2.5–3.5 mm. long, 2.5–3.0 mm. broad, the petioles 1.5–2.5 mm. long; cauline leaves linear to oblong, obtuse, slightly narrowed to the clasping base, 10–20 mm. long, ca. 1 mm. broad, the stipules entire, acicular, 0.5–1.0 mm. long. Inflorescences of terminal diffuse several-flowered cymes, the glabrous peduncles 10–25 mm. long; bracts ovate to narrowly lance-deltoid, 0.5–0.8 mm. long, scariose and transparent save for the darkened midrib; pedicels glabrous, 2–8 mm. long, at maturity usually longer than the flowers. Sepals 5, 1.5–2.2 mm. long, 0.5–0.7 mm. broad, minutely glandular, broadly oblong, apically obtuse, transparent save for the 3 ribs; petals 5, 2.0–2.5 mm. long, bifid about half their length, the lobes spatulate to narrowly oblong, trinerved, exappendiculate, merging imper-

ceptibly with the narrower claw; stamens (3?–) 5, ca. 2 mm. long, the oblong anthers ca. 0.4 mm. long; ovary at anthesis ellipsoid, slightly exceeded by the anthers, the slightly trifid style exceeding the anthers. Capsule ca. 1.8 mm. long, few seeded, the seeds cochleate, minutely tuberculate, ca. 0.6 mm. long. Fig. 6C (Holotype).

Chihuahua and Durango, Mexico.

Nelson 4813 is determined as this variety only with some misgivings. All the sepals are obtuse and cucullate and many of the pedicels are exceeded by the subtending bracts, in these respects approaching var. *depressa*. Although suggestive of var. *depressa*, this plant's upright habit and obovate 3-nerved petal-lobes deny this possibility.

18c. DRYMARIA EFFUSA var. **depressa** (Greene) J. Duke comb. & stat. nov.

Drymaria depressa Greene, Leafl. Bot. Obs. 1:153. 1905. (HOLOTYPE: *Metcalf 1430*; open glades of the Black Range, alt. 9,500 ft., N. Mex., ND; isotypes at F, GH, MO, UC, US, etc.!)

Drymaria minuscula Standl. & Steyerm. in Field Mus. Bot. 23:52. 1944. (HOLOTYPE: *Steyermark 50243*; on rocky limestone outcrops under *Juniperus standleyi*, alt. 3700 m., vicinity of Chémal, summit of Sierra de los Cuchumatanes, dept. Huehuetenango, Guatemala, F!)

Minute, subcespitose, glabrous to minutely puberulent annuals rarely to 5 cm. high, the branching largely confined to the base and the inflorescence. Rosette leaves orbicular to spatulate, 1.5–10.0 mm. long, 1–3 mm. broad; cauline leaves when present opposite, the blades oblong, 3–10 mm. long, 1–4 mm. broad, apically obtuse, basally tapered, subsessile, the stipules entire, 0.5–1.2 mm. long, acicular, caducous. Inflorescences of terminal lax (rarely condensed) several-flowered cymes, the bracts 1.5–2.0 mm. long, mostly longer than the pedicels, the pedicels and peduncles glabrous or glandular. Sepals 5, 1.5–2.5 mm. long, ca. 1 mm. broad, glabrous or glandular, oblong to ovate, apically obtuse, cucullate, 3-ribbed, the ribs subapically confluent; petals 5, 1.5–2.8 mm. long, bifid about half their length, the lobes linear to narrowly oblong, apically obtuse, usually 1-nerved, gradually tapering to the claw; stamens 5, 0.7–1.7 mm. long, the oblong anthers 0.2–0.3 mm. long; ovary at anthesis globose to obturbinate, the styles 2–3-fid about half their length, about equaling the anthers. Capsule ellipsoid to subglobose, about equaling the sepals, 6–12-seeded, the seed cochleate to lacrimiform, 0.5–0.7 mm. long, dorsally sulcate, minutely tuberculate. Fig 6A. (Isotype).

High altitudes, New Mexico, Colorado and Arizona, U. S. A., south to Guatemala.

As a rule this is quite a distinctive variety but it is probable that it hybridizes with other members of the series. *Metcalfe 1428* strongly suggests that hybridization has occurred with *D. leptophylla* or one of its varieties. Except rarely, *D. leptophylla* and *D. effusa* var. *depressa* are quite distinct, the former being characterized by an elongate subvirgate habit, the capsules shorter than the inner acute sepals, and the deeply cleft style, the latter being differentiated by the dwarf subcespitose habit, the capsules about equaling the obtuse, cucullate inner sepals, and the shallowly cleft style.

Fig. 6: A. *D. effusa* var. *depressa* (isotype); petal, 10×; sepal, 10×; stamen, 10×; flower, 10×; seed, 20×; habit, ¾×. B. *D. effusa* var. *effusa* (holotype); petal, 10×; sepal, 10×; stamen, 10×; seed, 15×. C. *D. effusa* var. *confusa* (holotype); petal, 10×; sepal, 10×; stamen, 10×; seed, 10×. D. *D. leptophylla* var. *cognata* (holotype); petal, 10×; sepal, 10×; stamen, 10×; seed, 15×. E. *D. leptophylla* var. *nodosa* (holotype); petal, 10×; sepal, 10×; stamen, 10×; seed, 15×. F. *D. leptophylla* var. *nodosa* (holotype of *D. gentryi*); petal, 15×; sepal 15×; stamen, 15×; seed, 15×. G. *D. leptophylla* var. *leptophylla* (isotype of *D. gracillima*); petal, 10×; sepal, 10×; stamen, 10×; seed, 15×.

In correspondence with Dr. Steyermark, I have suggested to him that *D. minuscula* probably represents an alpine reduction of what I here reduce to the var. *depressa*, and he tends to agree with this disposition of his diminutive species. The type from Guatemala has somewhat reduced nodes, leaves, sepals, etc., but such reductions also occur at the other end of the range of the variety, e.g. Colorado, and it seems doubtful that such diminutions are worthy of formal status.

19a. Drymaria leptophylla var. leptophylla

Drymaria leptophylla (Cham. & Schlecht.) Fenzl ex Rohrb. in Linnaea 37:195. 1871. (HOLOTYPE: *Schiede & Deppe 511*; ad radices montis Orizabae, B; *n.v.*)
Arenaria leptophylla Cham. & Schlecht. in Linnaea 5:233. 1830.
Drymaria tenella A. Gray, Pl. Fendl. 12. 1849. (HOLOTYPE: *Fendler 56*; eight miles west of las Vegas, New Mexico; GH!)
Drymaria nodosa var. ? *gracillima* Hemsl. Diag. Pl. Nov. 2:22. 1879. (HOLOTYPE: *Parry & Palmer 60*; in regione San Luis Potosi, alt. 6000–8000 ped., Mexico, K *n. v.*; isotypes at MO, GH, etc.!)
Drymaria gracillima (Hemsl.) J. N. Rose, in Contr. U. S. Nat. Herb. 5:132. 1897.

Erect delicate, usually sparsely branched annuals to as much as 20 cm. high, the internodes much longer than the leaves, glabrous to minutely glandular, the taproot ca. 1 mm. thick. Leaves opposite, rarely pseudoverticillate, glabrous, linear to narrowly oblong, 5–25 mm. long, 0.5–1.0 mm. broad, often involute and circinate, apically obtuse or acute, tapered to the subsessile base; stipules entire, 0.2–0.8 mm. long, acicular, caducous. Inflorescences of terminal many-flowered dichasial cymes, the peduncles 1–5 cm. long, glabrous to minutely glandular; bracts ovate, 0.5–1.0 (–1.5) mm. long, equaling or exceeding the pedicels. Sepals 5, ovate, 1.5–3.5 mm. long, narrowly ovate, apically acute and often somewhat reflexed (the outer sepals obtuse and cucullate in some northern material), 3-ribbed, glabrous or with a few sessile glands; petals 5, 1.2–2.4 mm. long, bifid about half their length, the lobes linear, obtuse or acute; stamens 5, 1.0–1.5 mm. long, the suborbicular anthers ca. 0.2 mm. long, the filaments basally and briefly connate; ovary at anthesis subglobose, the style about attaining the anthers, divided nearly to the base. Capsule 1.5–2.0 mm. long, 5–20-seeded, the seeds cochleate, 0.5–0.7 mm. long, evenly tuberculate with domical tubercles. Fig 6G (Isotype of *D. gracillima*).

Arizona to Colorado, U.S.A., south to southern Mexico, and in Baja California.

Toward the northern end of its range, the specimens belonging to the typical variety show frequent, but inconsistent, tendencies toward more obtuse, often cucullate, outer sepals and more pronouncedly coiled and contorted leaves. In the northern material the outer sepals are more frequently shorter than the inner, while the converse condition is more frequent toward the south. Although there is not enough material to justify any rigid hypothesis, I would guess that clinal variation is at work in this complex variety.

19b. Drymaria leptophylla var. **cognata** (S. F. Blake) J. Duke comb. & stat. nov.

Drymaria cognata S. F. Blake, in Journ. Wash. Acad. 14:285. 1924. (HOLOTYPE: *Palmer 912*, vicinity of Durango, Durango, US!)

Upright, diffusely branching, locally glandular-puberulent annual to as much as 15 cm. high. Leaves opposite, the blades 6–20 mm. long, 0.5–1.5 mm. broad, glabrous, lance-linear, apically acute, gradually tapering to the subsessile somewhat clasping base, veinless or obscurely 3-nerved; stipules mostly entire, acicular, 0.5–0.8 mm. long. Inflorescences of several-flowered, diffuse, trichotomous cymes, the axes locally glandular-puberulent; bracts lance-ovate to ovate, aristate, scariose save for the green excurrent midrib, 1–2 mm. long, usually shorter than the subtended pedicels, the pedicels 0.5–4.0 mm. long. Sepals 5, 3.3–4.5 mm. long, 0.8–1.3 mm. broad, glabrous or very sparsely glandular, lance-ovate, apically attenuate, 3-ribbed, transparent save for the green ribbed area; petals 5, 3.0–3.5 mm. long, bifid slightly more than half their length, the sinus broad, the lobes narrowly oblong, obtuse, the trunk flaring before tapering rather abruptly to the claw; stamens 5, 2.0–2.5 mm. long, the oblong anthers ca. 0.5 mm. long; ovary at anthesis subglobose, the style slightly shorter, trifid about half its length, slightly exceeding the anthers. Capsule ellipsoid, 2–3 mm. long, ca. 5-seeded, the seeds cochleate, ca. 0.8 mm. broad, minutely and regularly tuberculate. Fig. 6D (Holotype).

Durango and Chihuahua, Mexico.

19c. DRYMARIA LEPTOPHYLLA var. **nodosa** (Engelm.) J. Duke comb. nov.

Drymaria nodosa Engelm. in A. Gray, Pl. Fendl. 12. 1849. (HOLOTYPE: Plants grown from seed collected by Wislizenius in the mountains near Cosiquiriachi, MO!)
Drymaria tenella var. *nodosa* (Engelm.) Wiggins, in Proc. Cal. Acad. 4^{25}:205. 1944.
Drymaria gentryi Fosberg, in Proc. Biol. Soc. Wash. 62:147. 1949. (HOLOTYPE: *Gentry 2669*; transition pine slope, los Cascarones, Río Mayo; Chihuahua; US!; isotypes at MO, UC, etc.)

Erect delicate, sparsely branched annuals (or perennials?) to as much as 25 cm. high, the internodes mostly longer than the leaves, usually glandular-puberulent, the taproot to 2 mm. in diameter. Basal leaves spatulate to orbicular, opposite or pseudoverticillate, caducous; cauline leaves opposite, glabrous or minutely glandular, 5–30 mm. long, 0.5–2.5 mm. broad, 1-nerved, linear to narrowly elliptic, apically obtuse to apiculate, sessile; stipules entire, acicular, caducous, 0.5–1.5 mm. long. Inflorescences of terminal many-flowered dichasial cymes, the peduncles 2–5 cm. long, stipitate-glandular; bracts lance-deltoid to ovate, acuminate, 0.7–2.5 mm. long, mostly shorter than the pedicels, the pedicels stipitate-glandular, 0.5–5.0 mm. long. Sepals 5, subequal, 2.3–3.5 mm. long, 0.5–1.5 mm. broad, lanceolate to ovate, acuminate, basally or entirely stipitate-glandular, 3-ribbed, the ribs distally confluent; petals 5, 2.0–3.5 mm. long, bifid slightly more than half their length, the lobes linear to oblong or narrowly spatulate, obtuse, mostly 1-nerved, exappendiculate; stamens 5, 1.5–2.5 mm. long, the oblong anthers ca. 0.4 mm. long, the filaments basally connate, often with inconspicuous staminodial flaps; ovary at anthesis ellipsoid to subglobose, the styles elongate, nearly as long as the ovary, bifid or trifid less than half their length, equaling or exceeding the anthers. Capsule ellipsoid, 1.5–2.0 mm. long, shorter than the sepals, 1–9-seeded, the seeds cochleate, the anterior end strongly recurved, minutely and regularly reticulate, 0.6–1.0 mm. broad. Fig. 6E (Holotype of *D. nodosa*), Fig. 6F (Holotype of *D. gentryi*).

Chihuahua, Sonora, Durango, San Luis Potosi and Hidalgo, Mexico.

Gentry 2669, type of *D. gentryi*, stands out with its rather broad leaves, but examination of other specimens e.g. *LeSueur 623*, also from Chihuahua, shows that Fosberg's species cannot stand as distinct from *D. leptophylla* var. *nodosa*.

Equally aberrant are *S. S. White 4185* and *4776* from Sonora. In these specimens, the inflorescence is strikingly congested and the petal-lobes are broader than those of most specimens of the variety *nodosa*. In spite of the bizarre inflorescence, it seems best to retain them within the variety, with which they coincide in other fundamental characteristics.

I. Series TENUES

Leaves opposite, lanceolate, petiolate, stipulate, the stipules mostly lacerate. Flowers in monopodial or dichasial cymes, the pedicels longer or shorter than the bracts. Sepals acute, 1–3-nerved. Petals bifid, the lobes 1–5-nerved, unguiculate, exauriculate. Stamens 2–5. Seeds cochleate, tuberculate, the tubercles not ornate. Two diffusely spreading annual or perennial Mexican species. Fig. 7.

a. Sepals 3-ribbed, stipitate-glandular; ultimate branches of the cymes monopodial; petioles 0.5–1.5 mm. long.....20. D. ANOMALA

a. Sepals 1-ribbed, glabrous or with sessile glands; cymes predominantly dichasial; petioles 1–6 mm. long.....21. D. TENUIS

20. DRYMARIA ANOMALA S. Watson, in Proc. Am. Acad. 25:143. 1889. (HOLOTYPE: *Pringle 2847*, Carneros Pass, Coahuila, US!; isotype at GH)

Upright or spreading annuals or perennials, much branched from below, the internodes mostly longer than the leaves, stipitate-glandular, the taproot to 5 mm. thick. Cauline leaves opposite, 3–8 mm. long, 2–4 mm broad, glabrous to glandular or puberulent, the blades lance-elliptic, obscurely veined, apically acute, basally cuneate to acute, the petioles mostly less than 1 mm. long; stipules entire or bifid, lance-deltoid to acicular, persistent, 0.5–1.5 mm. long. Inflorescences of terminal many-flowered cymes, the first branches dichasial, subsequent branches becoming monopodial; peduncles 2–5 cm. long, glabrous to stipitate-glandular; bracts 0.5–2.0 mm. long, exceeding the pedicels, the pedicels stipitate-glandular or glabrescent. Sepals 5, 2–3 mm. long, 1.0–1.5 mm. broad, stipitate-glandular, broadly elliptic, apically acute, with 3 prominent veins, the outer submarginal, there being little or no scariose margin; petals 5, 1.5–2.0 mm. long, bifid a little over half their length, the lobes oblong, obtuse; stamens (2–) 3–5, 1.0–1.4 mm. long, the anthers oblong, ca. 0.3 mm. long; ovary at anthesis obturbinate, the style trifid about half its length, much shorter than the ovary, about attaining the anthers. Capsule about equaling the sepals, 5–9-seeded, the seeds cochleate, closely tuberculate, 0.6–0.9 mm. broad. Fig. 7A (details from Holotype).

Coahuila, Zacatecas, San Luis Potosi and Hidalgo, Mexico.

21. DRYMARIA TENUIS S. Watson, in Proc. Am. Acad. 25:142. 1889. (HOLOTYPE: *Pringle 2120*; under ledges of the barranca near Guadalajara, Jalisco, US!; isotype at GH)

Drymaria filiformis Robinson & Seaton, in Proc. Am. Acad. 28:117. 1893. not Benth. 1863. (HOLOTYPE: *Seaton 267*; barren slopes, Mt. Orizaba, 9000 ft. GH!; isotypes at US, MO, NY, etc.)

Drymaria tenuis α var. *genuina* Briq. in Ann. Cons. & Jard. Bot. Gen. 13:374. 1911.

Drymaria tenuis β var. *jaliscana* Briq. loc. cit. 374. 1911. (HOLOTYPE: *Pringle 4536*; Civitas Jalisco, in declivibus altis prope Guadalajara, G; *n. v.*; isotypes at MO, US, etc.!)

Erect or clambering delicate annuals or perennials to as much as 50 cm. long, the internodes much longer than the leaves, glabrous or pilosulous, the root sometimes lignescent, to as much as 6 mm. thick. Leaves opposite, glabrous, glandular or pilosulous, the blades lance-elliptic to ovate, apically and basally acute, 2.5–10.0 mm. long, 1–7 mm. broad, the petioles 0.5–5.0 mm. long; stipules lacerate, the divisions acicular, 0.5–2.0 mm. long. Inflorescences of terminal dichasial cymes, the peduncles very elongate, glabrous; bracts ovate, scariose, 1–2 mm. long, the

Fig. 7: A. *D. anomala* (details from holotype); inflorescence, 1×; flower, 10×; petal, 10×; stamen, 10×; seed, 15×. B. *D. tenuis* (holotype of *D. filiformis*); petal, 10×; sepal, 10×; stamen, 10×; seed, 22½×. C. *D. tenuis* (holotype); inflorescence, ¾×; flower and pedicels, 15×; petal, 20×.

pedicels 2–7 mm. long, glabrous, usually much longer than the subtending bracts. Sepals 5, the outer ovate, apically obtuse, 2.0–2.5 mm. long, ca. 1 mm. broad, the one rib occasionally excurrent; inner sepals narrowly ovate to ovate, 2.5–3.0 mm. long; petals 5, 1–2 mm. long, bifid about two-thirds their length, the lobes oblong, apically obtuse or acutish, exappendiculate, gradually tapering to the linear claw; stamens 5, 1.0–1.3 mm. long, the oblong anthers ca. 0.2 mm. long, the filaments basally connate; ovary at anthesis subglobose, ca. 0.8 mm. long; style bifid or trifid about half its length, about attaining the anthers. Capsule ovoid, about equaling the sepals, 5–15-seeded, the seeds cochleate, 0.5–0.7 mm. broad, evenly tuberculate, the dorsal tubercles mostly longer than broad. Fig. 7B (Holotype of *D. filiformis* Robinson & Seaton); Fig. 7C (Holotype of *D. tenuis*).

Michoacan, Jalisco, Guanajuato, Zacatecas and Veracruz, Mexico.

The type of *D. filiformis* from Mt. Orizaba differs only in having shorter petioles and smaller, more obtuse petal lobes, differences possibly resulting from the alpine environment and probably of no taxonomic consequence. Unfortunately Briquet relied too heavily on Watson's description of *D. tenuis* as glabrous, and published the variety *jaliscana*, believing it to differ in being pubescent. Examination of the holotype of *D. tenuis* reveals that Watson's description was erroneous; the type is locally villosulous with hairs up to 0.5 mm. long. Briquet's pubescent variety, collected very near the type locality of the typical variety, is probably no more pubescent than the typical variety.

J. Series FRUTESCENTES

Leaves linear to lanceolate, opposite, occasionally pergameneous, sessile or briefly petiolate, stipulate or estipulate. Flowers, showing tendencies toward monoecism, in dichasial bracteate cymes. Sepals acute, 3–5-ribbed. Petals bifid, the lobes 3–9-nerved, exauriculate, unguiculate or exunguiculate, the trunk entire or denticulate. Sepals cochleate, tuberculate, the tubercles acute or obtuse. Four more or less erect suffrutescent perennial species of Peru and Ecuador. Fig. 8.

a. Leaves neither imbricate nor pungent; pedicels and sepals often glandular, the sepals 3–4-nerved; petals not tapered to the claw.
  b. Pedicels and sepals usually glandular, the midrib of the sepals not excurrent; seeds with domical or conical tubercles; stipules present or absent. Peru and Ecuador.
    c. Leaves stipulate; trunk of the petals conspicuously constricted at the commissure with the lobes, the claw shorter than the trunk; seeds with acute conical tubercles. Ecuador.....22. D. STELLARIOIDES
    c. Leaves often estipulate; trunk of the petals more or less continuous with the lobes, the claw occasionally longer than the trunk; seeds with blunt, domical tubercles. Peru.....23. D. STEREOPHYLLA
  b. Pedicels and sepals glabrous, the midrib of the sepals excurrent; seeds with domical tubercles; stipules present. Peru.....24. D. AURICULIPETALA
a. Leaves imbricate, pungently acute; pedicels and sepals glabrous, the sepals mostly 5-nerved; petals tapered to the claw. Peru.....25. D. FRUTESCENS

22. DRYMARIA STELLARIOIDES Humb. & Bonpl. ex Roem. & Schult. Syst. Veg. 5: 406. 1819. (HOLOTYPE: *Humb. & Bonpl. s. n.*; crescit prope Hambato, alt. 1380 hex. [Regno Quitensi]; probably destroyed; fragment and photograph at F! illustr. HBK. Nov. Gen. & Sp. 6; *pl. 516.* 1823.)

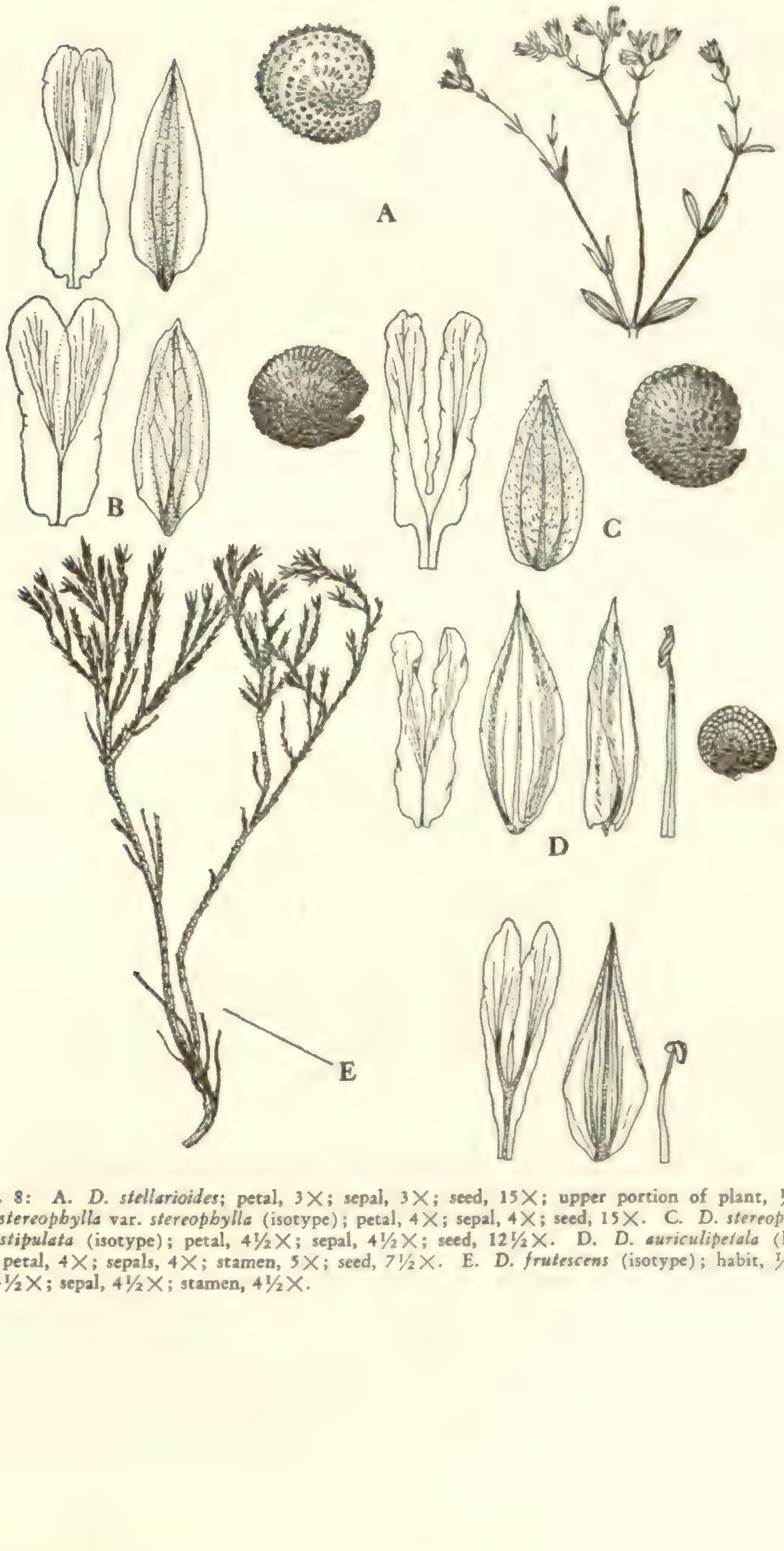

Fig. 8: A. *D. stellarioides*; petal, 3×; sepal, 3×; seed, 15×; upper portion of plant, ½×. B. *D. stereophylla* var. *stereophylla* (isotype); petal, 4×; sepal, 4×; seed, 15×. C. *D. stereophylla* var. *exstipulata* (isotype); petal, 4½×; sepal, 4½×; seed, 12½×. D. *D. auriculipetala* (holotype); petal, 4×; sepals, 4×; stamen, 5×; seed, 7½×. E. *D. frutescens* (isotype); habit, ⅓×; petal, 4½×; sepal, 4½×; stamen, 4½×.

Upright or ascending dichotomous lignescent perennials from a stout taproot to 15 mm. thick, the internodes mostly longer than the leaves except on condensed lateral branches, glabrous to glandular-pubescent. Leaves opposite, glabrous or rarely glandular-puberulent, lanceolate to oblanceolate, apically acute, marginally entire, 3-ribbed, 5–20 mm. long, 2.5–7.5 mm. broad, tapered to the sessile, clasping base; stipules entire, apparently fused or occasionally absent, 0.0–2.5 mm. long. Inflorescences of lax to crowded 5–many-flowered cymes, the peduncles 1–8 cm. long; bracts lanceolate, 3–5 mm. long, intergrading with the foliage leaves; pedicels glabrous to densely glandular-puberulent, all but the central pedicel usually exceeded by the bracts. Sepals 5, narrowly to broadly lanceolate, glabrous to densely glandular-puberulent, strongly 3-ribbed, apically acute, (4–) 5–9 mm. long, 2–3 mm. broad; petals 5, 5–10 mm. long, bifid about half their length, the lobes oblong, obtuse, 4–8-nerved, exauriculate, constricted slightly toward the trunk, the trunk rhombic to rectangular, truncate to the short claw; stamens 5, 3–6 mm. long, those of fertile flowers (destined to mature seeds) usually much shorter than those of infertile flowers; anthers 0.7–1.1 mm. long; filaments basally connate into a cup ca. 1 mm. deep; ovary (occasionally absent in flowers with long stamens) ellipsoid, multiovulate, those of fertile flowers about equaling the anthers; styles 1.5–3.0 mm. long, trifid for about one-fourth their length. Capsule ellipsoid, substylopodiate, 3–5 mm. long, 2–many-seeded, the seeds laxly circinnate, 0.8–1.2 mm. broad, tuberculate, the dorsal tubercles subspinulose, the facial tubercles tending to be polygonal. Fig. 8A.

Ecuador.

Pachano 95 (Fig. 8A) and the isotype seem to differ from other representatives of this species in that the sepals and petals are unusually long and the petal lobes have more numerous veins. Seeds of this species, as illustrated in HBK. Nov. Gen. & Sp. 6: *pl. 516.* 1823, appear to be constantly subspinulose-tuberculate. There is no indication in the aforementioned illustration however of the polygamous tendency which I believe characterizes this species. Although the material available for dissection has not been too copious, I feel that certain correlates exist in different types of flowers. Many of the ovaries bear aberrant ovules and in some flowers the ovary is completely lacking. In flowers which mature seed, the anthers rarely surpass the body of the capsule, while in those flowers with aberrant ovules, the filaments seem to have elongated so that the anthers equal or surpass the style branches. In some unnumbered specimens collected by Jameson near Cuenca and Loxa, there are flowers with long glandular sepals and others with shorter glabrous sepals; those with the shorter glabrous sepals proved to be fertile while some of those with longer glandular sepals were completely devoid of ovaries.

23. Drymaria stereophylla Mattf. in Notizbl. Bot. Gart. Berl. 13:436. 1936. (holotype: *Raimondi 2502*; Peru. Dep. Junin: Prov. Jauja; Abhang am Fusse des Chacapalpa zwischen Huari und Jauja, B, *n. v.*; probably destroyed)

Drymaria stereophylla Mattf. ex MacBride, in Field Mus. Bot. 13^2:626. 1937. (holotype: *MacBride 962*; Junin; in crevices of limestone cliffs, 4000 m., La Oroya, Peru; F!; isotype at US)

Drymaria stereophylla var. *exstipulata* Mattf. in Notizbl. Bot. Gart. Berl. 13:437. 1936. (HOLOTYPE: *Weberbauer 6600*; Peru; Dep. Junin; nordöstlich von Huancayo unterhalb der Hacienda Acopalca, geogr. Br. 12° 5′ S., an Felsen, 3600–3700 m ü. M.; B, *n. v.*; isotypes at F, MO, US!)

Laxly spreading or ascending lignescent perennials to as much as 35 cm. tall, the internodes shorter to longer than the leaves, glandular-puberulent, the taproot to as much as 1 cm. thick. Leaves opposite, 4–12 mm. long, 2–6 mm. broad, glandular-puberulent, broadly lanceolate to narrowly ovate, apically acute to aristately acuminate, subsessile, the brief petioles clasping; stipules entire, lance-linear, caducous, 0.5–1.0 mm. long, absent in the variety. Inflorescences of lax occasionally congested terminal 3–many-flowered cymes, the peduncles 1–6 cm. long; bracts lanceolate to lance-ovate, 3–5 mm. long, the pedicels 2–10 mm. long, stipitate-glandular. Sepals 5, 5.0–7.5 mm. long, 2.0–4.5 mm. broad, glandular, ovate, 3–4-nerved, the midrib not excurrent, the outer acute, the inner obtuse; petals 5, 5–9 mm. long, deeply bifid, the lobes oblong, obtuse, 5–8-nerved, exappendiculate, not constricted at the junction with the trunk, the trunk truncate to the claw; the claw minute, or, in the variety, as long as the trunk; stamens 5, 4–6 mm. long, the oblong anthers ca. 1 mm. long, the filaments basally connate forming a cup about 1 mm. deep; ovary at anthesis turbinate to ellipsoid, the style 1.0–2.5 mm. long, bifid or trifid about one-third its length. Capsule ovoid, 2.5–3.5 mm. long, 4–27-seeded, the seeds loosely circinnate, 0.9–1.3 mm. broad, tuberculate, the tubercles low and contiguous. Fig. 8B (Isotype of var. *stereophylla*); Fig. 8C (Isotype of var. *exstipulata*).

Departments Junin, Cuzco and Lima, Peru.

Mattfield commented on the homogeneity of the specimens which he cited in the original description of *D. stereophylla* var. *exstipulata*. Material collected subsequently has further substantiated the differences in the varieties and other differences have been uncovered. The shape of the petals, frequent telescoping of the internodes, and the absence of stipules in the var. *exstipulata* are characteristics which point toward the bizarre *D. frutescens*. The two varieties of *D. stereophylla* may be keyed as follows:

a. Stipules present, the leaves rigid, glabrous or with a few sessile glands; trunk of the petals much longer than the claw, the claw occasionally not even apparent.....var. STEREOPHYLLA

a. Stipules absent, the leaves not rigid, plants often densely stipitate-glandular; claw of the petals about as long as the trunk, obvious.....var. EXSTIPULATA

24. DRYMARIA AURICULIPETALA Mattf. in Notizbl. Bot. Gard. Berl. 13:439. 1936. (HOLOTYPE: *MacBride & Featherstone 2264*; Peru; Llata, von Felsbändern herabhängend, ca. 2100 m ü. M.; F!; isotypes at GH, MO, US)

Upright or ascending glabrous suffruticose annuals or perennials to as much as 60 cm. long. Leaves opposite, glabrous, 5–15 mm. long, 1.5–3.0 mm. broad, the blades narrowly lanceolate, slightly falcate, apically attenuate, aristate, basally clasping, the stipules entire, acicular, tardily deciduous, 1.0–1.5 mm. long. Inflorescences of lax terminal 1–7-flowered cymes, the glabrous peduncles 5–40 mm. long; bracts broadly ovate, strongly 1-ribbed, 2.5–3.5 mm. long, exceeding the pedicels. Sepals 5, subequal, 7–8 mm. long, 2–3 mm. broad, glabrous or minutely glandular,

lanceolate, apically attenuate and aristate, basally unguiculate or umbonulate, only the midrib conspicuous; petals 5, 6.5–7.5 mm. long, bifid about half their length, the lobes broadly oblong, apically rounded, 1.0–1.3 mm. broad, 4–6-nerved, exapendiculate, hardly constricted at the junction with the trunk, the trunk 1.2–1.6 mm. broad, the claw minute; stamens 5, ca. 5.5 mm. long, the oblong anthers ca. 0.8 mm. long, often somewhat twisted; ovary at anthesis obovoid, slightly exceeded by the anthers, the style trifid about half its length, about equaling the anthers. Capsule ca. 4 mm. long, many-seeded, the seeds cochleate, ca. 1 mm. broad, dorsally flattened or sulcate, tuberculate, the tubercles low and contiguous. Fig. 8D (Holotype).

Known only from the type locality; Llata, Peru.

25. Drymaria frutescens Mattf. in Notizbl. Bot. Gart. Berl. 13:439. 1936. (holotype: *Weberbauer 7203*; Peru; Dep. Libertad, Prov. Santiago de Chuco, über der Hacienda Angasmarca; Grassteppe mit zahlreichen eingestreuten Sträuchern, an felsigen Abhängen, 3650 m ü. M.; B, *n. v.*; isotypes at F, US!)

Ascending frutescent glabrous perennials to 30 cm. tall, the leaves closely appressed to the stems. Leaves 2–6 mm. long, 1.0–1.5 mm. broad, imbricate in two ranks, lance-ovate, apically aristate-acuminate, basally clasping, 3-ribbed, marginally transparent; stipules entire, narrowly lance-deltoid, ca. 0.5 mm. long. Flowers solitary at the ends of the branches, the bracts similar to the foliage leaves, the glabrous pedicels 2–3 mm. long. Sepals 5, subequal, 5.5–7.0 mm. long, 1.5–2.0 mm. broad, glabrous concavo-convex, ovate, apically acute or shortly acuminate, transparent save for the 7 nerves; petals 5, 5–7 mm. long, bifid for about two-thirds their length, the lobes oblong to spatulate, obtuse or emarginate, exappendiculate, the trunk and claw merging almost imperceptibly; stamens 5, 2.5–4.5 mm. long, the oblong anthers ca. 0.8 mm. long, often spirally contorted in drying; ovary at anthesis ellipsoid, exceeded by the anthers, the style trifid about half its length, about equaling the anthers. Capsule 2.5–3.0 mm. long; mature seeds not seen. Fig. 8E (Isotype).

Known only from the type locality in Dept. Libertad, Peru.

K. Series fasciculatae

Leaves opposite, linear-elliptic to narrowly ovate, subsessile, stipulate, the stipules entire or bifid. Flowers in rather dense bracteate cymes, the bracts often stipulate. Sepals acute, 1–3-nerved. Petals bifid, the lobes 1–3-nerved, exauriculate, the claw minute or completely absent (except in *D. praecox*), the trunk as wide as the combined width of the lobes. Stamens 3–5. Seeds loosely or tightly cochleate, tuberculate. Three species in Peru, two rather delicate and minute annuals and the more or less suffrutescent *D. fasciculata*. Fig. 9.

a. Plants upright, often suffrutescent; sepals 5–8 mm. long; leaves mostly larger than 6 mm. long and 4 mm. broad; bracts not stipulate.....26. D. fasciculata
a. Minute depressed or ascending annuals; sepals 2.0–4.5 mm. long, glabrous, glandular or villosulous; leaves mostly less than 6 mm. long and 4 mm. broad; bracts often stipulate:

b. Sepals acuminate, glabrous, apically reflexed in age; herbage occasionally glandular but not villose. Dept. Lima, Huancavelica and Puno: Peru.....27b. D. ENGLERIANA var. DEVIA
b. Sepals acute, stipitate-glandular, occasionally apically inflexed; herbage villose or villosulous. Dept. Ancash and Cuzco; Peru:
c. Petals with a broad trunk, not tapered to a claw, the lobes 1–3-nerved; pedicels of the central flowers about as long as their bracts. Dept. Ancash.....
.....27a. D. ENGLERIANA var. ENGLERIANA
c. Petals gradually tapered to a definite claw, the lobes 2–4-nerved; pedicels of the central flowers much longer than their bracts. Dept. Cuzco.....28. D. PRAECOX

26. DRYMARIA FASCICULATA A. Gray, Bot. U. S. Expl. Exped. 125. 1854. (HOLOTYPE: *Wilkes exped. s. n.*; Andes of Peru, near Obrajillo, US!)

Upright dichotomous, paucifoliate annuals to as much as 25 cm. high, subglabrous except for the glandular axes of the inflorescence, the taproot to as much as 3 mm. broad. Leaves opposite, the blades 8–18 mm. long, 4–10 mm. broad, ovate (the lowermost occasionally spatulate), apically acute or acuminate, marginally somewhat undulate, basally clasping, only the midrib obvious, the stipules entire, linear-lanceolate, caducous, ca. 1 mm. long. Inflorescences of terminal fasciculate, strongly dichotomous, 3–many-flowered cymes, the glabrous to densely glandular peduncles 2–6 cm. long, the bracts lanceolate to ovate, acute or mucronate, transparent save for the midrib, 4–6 mm. long, 2–4 mm. broad, obscuring the short pedicels. Sepals 5, subequal, 4–7 mm. long, 1.0–1.8 mm. broad, lance-oblong to narrowly elliptic, acuminate, rather strongly 3-ribbed, often with a scariose margin; petals 5, 2.5–7.0 mm. long, bifid about half their length, the lobes oblong, apically rounded to emarginate, 2–3-nerved, their outer margins forming straight lines with the margins of the trunk, exappendiculate, the trunk exunguiculate or subexunguiculate; stamens 5, 2–6 mm. long, the oblong anthers 0.4–1.2 mm. long; ovary at anthesis subcylindric, slightly exceeded by the anthers, the barely trifid style slightly exceeding the anthers. Capsule narrowly ellipsoid, included, 3–4 mm. long, several-seeded, the seeds laxly circinnate, minutely and rather evenly tuberculate, the anterior end usually long and pointed. Fig. 9A (details from Holotype).

Andes of Peru.

27a. DRYMARIA ENGLERIANA var. ENGLERIANA

Polycarpon englerianum Muschler, in Bot. Jahrb. 45:452. 1911.
(HOLOTYPE: *Weberbauer 3101*; Peru; Ancash; Huaraz, 4300 m.; probably destroyed at B; isotypes at F, G!)
Drymaria engleriana (Muschler) Baehni & MacBride, in Field Mus. Bot. 13²:621. 1937.

Minute prostrate annuals to 5 cm. high, the internodes mostly longer than the leaves, hirsutulous. Leaves opposite, the blades 2–8 mm. long, 1.0–4.5 mm. broad, ovate, apically acute, marginally entire, basally attenuate to the alate clasping petioles, weakly 3-nerved, scantily hirsutulous, the stipules entire or bifid, the divisions filiform to lance-deltoid. Inflorescences of terminal, rather lax, several-flowered cymes, the axes hirsutulous, the bracts 1.5–3.0 mm. mostly longer than the pedicels. Sepals 5, 2.0–3.6 mm. long, 0.6–1.2 mm. broad, narrowly ovate, apically acute or briefly acuminate, often with sessile or stipitate glands, 3-ribbed, only the midrib prominent, the apex not reflexed, often inflexed; petals 5, 1.0–2.4 mm. long,

Fig. 9: A. *D. fasciculata* (details from holotype); petal, 4×; sepal, 4×; stamen, 7½×; seed, 12½×; habit, ½×. B. *D. engleriana* var. *devia* (holotype); petal, 10×; sepal, 10×; seed, 20×. C. *D. engleriana* var. *engleriana* (holotype); petal, 10×; sepal, 10×. D. *D. praecox* (holotype); habit, 1×; petal, 7½×; sepal, 7½×; seed, 17½×.

bifid about half their length, the lobes obtuse to acute, oblong, 1-nerved, the outer margin forming more or less a straight line with the margin of the trunk, the claw not apparent; stamens 3–5, 1.0–1.5 mm. long, the suborbicular to oblong anthers ca. 0.2 mm. long, the filaments basally connate into a minute carnose column; ovary renoid, the style shorter than the ovary, ca. 0.5 mm. long, trifid about half its length. Capsule globose to ellipsoid, included, 1.5–2.0 mm. long, 2–8-seeded, the seeds laxly circinnate, minutely and evenly tuberculate, 0.7–0.9 mm. broad. Fig. 9C (Isotype).

High altitudes, Dept. Ancash, Peru.

Although Baehni and MacBride (in Field Mus. Bot. 13^2:621. 1937) correctly transferred this species to *Drymaria* from *Polycarpon*, MacBride (p. 627) also retains it as a species of *Polycarpon*, curiously stating that it is "probably only a densely cespitose form of *P. apurense*."

27b. DRYMARIA ENGLERIANA var. **devia** (Baehni & MacBride) J. Duke comb. & stat. nov.

Drymaria devia Baehni & MacBride, in Field Mus. Bot. 13^2:620. 1937. (HOLOTYPE: *Pennell 14655*; Lima; open rocky slopes near Canta, 4000 m., F!)

Delicate prostrate or ascending subglabrous annuals usually less than 5 cm. tall, branching mostly from the base. Leaves opposite, the blades 2.5–5.0 mm. long, 2–3 mm. broad, subcoriaceous, ovate, occasionally glandular, apically acute or attenuate and apiculate, basally clasping, the uppermost rather strongly 3-ribbed; stipules entire or bifid, the divisions narrowly lance-deltoid, ca. 1 mm. long. Inflorescences of dense terminal 1–11-flowered cymes, the glabrous peduncles 4–8 mm. long, the bracts 2–3 mm. long, ca. 1 mm. broad, ovate, aristate-acuminate, the midrib often cyanic; pedicels mostly less than 1 mm. long, concealed by the bracts. Sepals 5, 4.0–4.5 mm. long, 1.5–2.0 mm. broad, narrowly ovate, aristate-acuminate, strongly 3-ribbed, glabrous to minutely glandular, transparent save for the ribs; petals 5, 2.5–3.0 mm. long, bifid about half their length, the lobes oblong, obtuse, 1-nerved, curving outwardly to the inflated trunk, the trunk ca. 1.2 mm. broad, exappendiculate, the claw not apparent; stamens 5, ca. 2.2 mm. long, the oblong anthers ca. 0.4 mm. long; ovary at anthesis slightly exceeding the anthers, the style trifid about half its length. Capsule 2.5–3.0 mm. long, ca. 8-seeded, the seeds dorsally flattened, minutely tuberculate, ca. 0.6 mm. broad, dark brown. Fig. 9B (Holotype).

At high altitudes in Depts. Lima, Puno and Huancavelica, Peru.

This diminutive variety is closely related to the preceding and seems sufficiently distinct to warrant varietal recognition. The acuminate often reflexed, strongly ribbed sepals and the lack of jointed hairs seem to characterize the few specimens of the variety examined.

28. DRYMARIA PRAECOX Baehni & MacBride, in Field Mus. Bot. 13^2:625. 1937. (HOLOTYPE: *Weberbauer 6916*; between Pisac & Paucartambo, prov. Paucartambo, Dept. Cuzco, 4100 m., Peru, F!; isotypes at MO, US, etc.)

Delicate, virgate, glandular-puberulent annuals to as much as 5 cm. high, with few nodes below the inflorescence, the basal rosette often persistent. Basal leaves

spatulate; cauline leaves opposite, the blades 2–4 mm. ling, 1.5–3.0 mm. broad; villosulous, ovate, apically acute, basally clasping, obscurely trinerved, the stipules entire, acicular, 0.5–0.8 mm. long. Inflorescences of diffuse 1–9-flowered cymes, the axes densely glandular-puberulent; bracts ovate to lanceolate, stipitate, 1-ribbed, the rib often excurrent, 1.0–1.5 mm. long, the pedicels usually much longer. Sepals 5, 2.5–3.5 mm. long, 1.0–1.4 mm. broad, glandular-pubescent, narrowly ovate, apically acute or obtuse, often inflexed, 3-ribbed, transparent save for the ribs; petals 5, ca. 3 mm. long, bifid half their length or more, the lobes oblong, obtuse, exappendiculate, 3-nerved, gradually tapering to the base, the trunk and claw not discernibly differentiated; stamens 5, 1.2–1.5 mm. long, the suborbicular anthers ca. 0.3 mm. long; ovary at anthesis compressed-globose, exceeded by the anthers, about as long as the style; style trifid about half its length, slightly exceeding the anthers. Capsule included, ca. 2.2 mm. long, ca. 5-seeded, the seeds cochleate, ca. 0.7 mm. broad, tuberculate, the tubercles rather prominent, nearly contiguous. Fig. 9D (Holotype).

Known only from the type collection from Cuzco, Peru.

Perhaps a misfit in this series, this species may be of hybrid origin, and in some respects it recalls *D. glandulosa* var. *galeottiana*, perhaps also of hybrid origin.

L. Series DEBILES

29. DRYMARIA DEBILIS Brandegee, in Proc. Cal. Acad. 2^2:131. 1889. (HOLOTYPE: *Brandegee s. n.*; Purisima, Feb. 13, 1889; UC!)

Drymaria polystachya Brandegee, in Zoe 2:70. 1891. (HOLOTYPE: *Brandegee 35*; cliffs near San José del Cabo, Baja California; UC!; isotypes at D, US, etc.)

Drymaria diffusa J. N. Rose, in Contr. U. S. Nat. Herb. 1:130. *pl. 12*. 1892. (HOLOTYPE: *Palmer 819*; Carmen Island; US!; isotypes at F, MO, US, NY, etc.)

Drymaria polystachya var. *diffusa* (Rose) Wiggins, in Proc. Cal. Acad. 4^{25}:198. 1944.

Ascending or clambering, occasionally subscandent annuals or perennials, the tenuous, villose or glandular internodes shorter to longer than the leaves, the taproot to as much as 15 mm. thick. Leaves opposite, the blades 3–20 mm. long, 3–20 mm. broad, villose or glandular, broadly ovate to reniform, apically acutish and apiculate, basally cordate, often drying with a yellowish tinge, the petioles nearly as long as the blades, the stipules mostly entire, filiform, 1–3 mm. long. Inflorescences of terminal lax 3–many-flowered cymes, the axes villose or glandular puberulent, the peduncles 1–10 mm. long; bracts narrowly to broadly ovate, scariose, 1.5–2.5 mm. long, much exceeded by the pedicels, the villose or glandular pedicels to as much as 25 mm. long. Sepals 5, 2.5–5.5 mm. long, 1.5–2.4 mm. broad, glandular to villose, oblong to elliptic or ovate, apically obtuse, emarginate or with the midrib occasionally excurrent, the venation obscurely dichotomous and reticulate; petals 5, 3.0–6.5 mm. long, bifid about half their length, the lobes oblong, rounded to truncate at the apex, 1–2-nerved, gradually tapered to the claw; stamens 5, 1.0–3.5 mm. long, the filaments usually dimorphic, two or three being distinctly longer than the others, the anthers oblong 0.5–1.0 mm. long; ovary at anthesis ellipsoid, often stipitate, exceeded by the anthers, the style 1–2 mm. long, trifid to half its length. Capsule ellipsoid to ovoid, 1.0–3.5 mm. long, 6–

Fig. 10: A. *D. debilis* (holotype of *D. polystachya*); petal, 7½×; sepal, 7½×; seed, 20×; habit, ½×. B. *D. debilis* (holotype of *D. diffusa*); petal, 6×; sepal, 6×; seed, 20×. C. *D. debilis* (holotype); petal, 5×; sepal, 5×; stamen, 5×; seed, 10×. D. *D. laxiflora* (isotype of *D. chihuahuensis*); habit, ½×; petal, 6×; sepal, 6×; seed, 20×. E. *D. laxiflora* (isotype); petal, 5×; sepals, 5×; seed, 20×.

15-seeded, the seeds ampulliform, 0.6–1.0 mm. broad, the pointed anterior ends not strongly recoiled, the tubercles low, polygonal, rather remote. Fig. 10A (Holotype of *D. polystachya*); Fig. 10B (Holotype of *D. diffusa*); Fig. 10C (Holotype of *D. debilis*).

Baja California, Mexico.

This polymorphic species has generally been regarded as three separate species, the more or less sympatric differences purported to reside in the duration, pubescence, and the length and shape of the sepals and petals. I am more impressed by the homogeneity of certain other characters (e.g. the peculiar retort-shaped seeds, the inequality of the stamens, the venation of the sepals) than by the differences supposed to separate the three species. Particularly suspicious to me are keys in which the primary dichotomy is annual vs. perennial. Many *Drymaria* species, originally described as annual, have turned out to have perennial representatives. I prefer to think of *D. debilis* as a species embracing many contrasting characteristics, but with few, if any, correlated contrasts.

M. Series LAXIFLORES

30. DRYMARIA LAXIFLORA Benth. Pl. Hartw. 73. 1839. (HOLOTYPE: *Hartweg 523*; Guatemala; in rupibus Sunilo, BM? *n. v.*; isotypes at GL, F, LE, P, etc!)

Drymaria chihuahuensis Briq. in Ann. Cons. & Jard. Bot. Gen. 13: 370. 1911. (HOLOTYPE: *Pringle 331*; Mexicum: Civitas Chihuahua in rupibus umbrosis prope Chihuahua; G, *n. v.*; isotypes at F, GH, MO, NY, P, US, etc.!)

Glabrous to densely stipitate-glandular diffuse to subcespitose perennials to as much as 30 cm. high, the internodes mostly longer than the leaf-blades, the taproot to as much as 6 mm. thick. Leaves opposite, the blades glabrous to densely stipitate-glandular, ovate to reniform, 4–12 mm. long, 3–14 mm. broad, trinerved, apically obtuse to acute and mucronulate, marginally entire, basally acute to subcordate, the petioles 1–5 mm. long, the stipules bifid or trifid, rarely entire, the divisions setaceous, 0.5–3.5 mm. long. Inflorescences of lax few-flowered cymes, the peduncles 5–40 mm. long; bracts ovate, strongly 1-ribbed, scariose, apiculate, 1.5–3.0 mm. long, transparent save for the midrib, mostly shorter than the pedicels, the pedicels subglabrous to densely stipitate-glandular, 2–6 mm. long. Sepals 5, 2.5–6.0 mm. long, 1.5–2.2 mm. broad, glabrous to densely stipitate-glandular, lanceolate to narrowly ovate, trinerved, acute, the midrib occasionally excurrent, the laterals often subapically dissipating; petals 5, 2.5–6.0 mm. long, bifid one-half to two-thirds their length, the lobes oblong, apically emarginate, with one dichotomous vein, exappendiculate, continuous with the trunk, the trunk as long as or longer than the claw; stamens 4–5, 2–4 mm. long, the oblong anthers 0.3–0.8 mm. long; ovary at anthesis ellipsoid, exceeded by the anthers, the elongate style trifid one-third to one-half its length, slightly exceeding the anthers. Capsule 3–4-valved, 2–4 mm. long, many-seeded, the seeds 0.5–0.7 mm. broad, evenly tuberculate, the dorsal tubercles conical, the facial tubercles substellate. Fig 10D (Isotype of *D. chihuahuensis*); Fig. 10E (Isotype of *D. laxiflora*).

Texas through continental Mexico to Guatemala, to the south becoming less glandular and tending to have larger floral parts.

Examination of several isotypes of *Hartweg 523* from Guatemala reveals that the plant, although described as glabrous, possesses a few scattered stipitate glands. *Bernoulli & Cario 3255* at Leningrad, collected in Quezaltenango, matches the types of *D. laxiflora* in all respects except that it is more glandular. Toward the northern end of the range, the species has some very glandular representatives whose seeds are nearly black, pleiochroistic and very ornately sculptured. In spite of the extreme variation, some of which appears to be along a north–south cline, only one species seems to be involved. *Bourgeau 2946* and *Rose & Hay 5676* from Mt. Orizaba have petals, the lobes of which are so deeply emarginate as to recall the twice dichotomous petals of *D. longepedunculata*, and it is here suggested that the Series LAXIFLORES is genetically closely related to the Series EXCISAE.

N. Series VILLOSAE

Leaves opposite, stipulate, mostly long-petiolate, and ovate to orbicular, often villose. Flowers in few–many-flowered cymes, rarely subsolitary in the axils. Sepals acute or obtuse, 1–3-nerved. Petals (occasionally absent) merely bifid, the lobes usually ciliate-auriculate, 1–7-nerved, unguiculate. Stamens 3–5. Seeds cochleate, tuberculate, the tubercles stellate, cylindric or capitate. Four species of continental Mexico, Central and South America, one introduced in Malaysia. Figs. 11 and 12.

a. Sepals subdeltoid, glabrous, unctuous; petals with 2–4 filiform auricles on either side; leaves narrowly to broadly orbiculate, not basally cordate; stipules entire, lanceolate; Mexico to Costa Rica.....31. D. MULTIFLORA

a. Sepals lanceolate to ovate or oblong to orbicular, glabrous, glandular or villose, occasionally unctuous; petals with 0–6 filiform auricles on either side; leaves ovate to reniform, rarely orbicular, occasionally cordate; stipules entire or lacerate, the divisions filiform to lanceolate.

b. Sepals and petals 3.5–7.0 mm. long; leaves cordate, 10–30 mm. broad. Mexico.

c. Stipules longer than the petioles; pedicels glandular-puberulent; midrib of the outer sepals excurrent; petals with 1 ciliate auricle on either side.....32. D. CONZATTII

c. Petioles longer than the stipules; pedicels villose; midrib of the outer sepals subapically dissipated; petals with 3–6 ciliate auricles on either side.....33. D. MALACHIOIDES

b. Sepals 1.6–3.8 mm. long, the petals rarely to 4 mm. long, but then divided nearly to their base; leaves ovate to reniform, occasionally with cordate bases, 5–15 mm. broad. Mexico to South America; Malaysia.

d. Sepals elliptic, acute (rarely obtuse, but then rather strongly trinerved); petals, when present, divided about half their length, with 1–4 linear auricles on either side; capsule not or but slightly longer than the sepals; plants villose or hirsute. Mexico to Peru; Malaysia.....34a. D. VILLOSA ssp. VILLOSA

d. Sepals oblong to orbicular, obtuse; petals, when present, divided halfway or almost completely to their base, the auricles, when present, deltoid to filiform, if filiform the petals divided nearly to the base; capsule often twice as long as the sepals; plants glabrous to villose. Mexico to Peru, lacking in southern Central America:

e. Sepals glabrous; petals occasionally auriculate, often divided nearly to the base; tubercles of the seeds stellate or capitate, the dorsal tubercles often longer than broad. Mexico to Peru.....34b. D. VILLOSA ssp. PALUSTRIS

e. Sepals villose; petals exauriculate, divided about half their length; tubercles of the seeds stellate, the dorsal tubercles rarely longer than broad. Venezuela, Colombia. .....34c. D. VILLOSA ssp. PARAMORUM

31. DRYMARIA MULTIFLORA Brandegee, in Zoe 5:232. 1906. (HOLOTYPE: *Purpus 1653*; dry hills, Salto de Agua, Mexico, UC!; isotypes at F, GH, MO, US, etc.)

Erect or ascending perennials to as much as 50 cm. tall, much branched, the internodes mostly longer than the leaves, glabrous to stipitate-glandular, rarely villosulous. Leaves opposite, the blades glabrous, 4–22 mm. long, 4–25 mm. broad, broadly deltoid-ovate, orbicular or reniform, apically rounded to deeply emarginate, marginally entire, basally truncate to acute, not cordate, weakly 3–5-nerved; petioles 2–20 mm. long, the stipules entire, lanceolate, 1.0–2.5 mm. long. Inflorescences of terminal 3–many-flowered cymes, the peduncles to as much as 10 cm. long, often stipitate-glandular; bracts ovate, 2.5–5.0 mm. long, the pedicels mostly 5–22 mm. long, glabrous or stipitate-glandular. Sepals 5, glabrous, unctuous, rarely with sessile glands, lance-deltoid to deltoid-ovate, apically acute, at least by extension of the midrib, 3–6 mm. long, 1.2–2.0 mm. broad, often saccate basally; petals 5, 2.5–7.0 mm. long, usually equaling or exceeding the sepals, bifid about two-thirds their length, the lobes apically rounded, oblong 2–5-nerved, basally provided with ca. 3 ciliate auricles; stamens 3–5, 2.0–3.5 mm. long, the oblong anthers 0.3–0.5 mm. long; ovary at anthesis globose to ovoid, the style 1–2 mm. long, bifid or trifid about half its length. Capsule 2.0–3.5 mm. long, ovoid, 4–26-seeded, the seeds ca. 1 mm. broad, the dorsal tubercles longer than broad, the facial tubercles substellate. Fig. 11A (Isotype).

Sinaloa, Mexico, to Costa Rica.

Standley 83478 from Quezaltenango is highly aberrant. Many flowers are apetalous; others have entire liguliform petals; two flowers had twice-dichotomous petals suggestive of *D. longepedunculata*.

32. DRYMARIA **conzattii** J. Duke sp. nov.

Plantae annuae erectae vel diffusae glanduloso-villosae usque ad 45 cm. altae internodis saepe quam foliis longioribus. Folia opposita glanduloso-villosa reniforma apice vix acuminata basi cordata leviter 5–7 nervata, 5–20 mm. longa, 5–30 mm. lata, petiolis brevibus ad 2.5 mm. longis. Stipulae integrae vel laceratae lobis filiformibus quam petioli longioribus. Inflorescentiae terminales axillaresque in confertas 3–11-floriferes cymas dispositae rhachide glanduloso-villoso bracteis ovatis 3.0–4.5 mm. longis costis excurrentibus quam pedicellis longioribus. Sepala 5 externa minuta glanduloso-puberula angusto-ovata acuta conspicue 3-costata, 5.0–5.6 mm. longa, 1.8–2.0 mm. lata, interna paulo breviora paene glabrescentia; petala 5, 4.0–4.5 mm. longa 3/4-bifida lobis oblongis obtusis gradatim ad angusto-oblongum unguem constrictis basi ciliatis; stamina 5, 3.0–3.5 mm. longa antheris oblongis ca. 0.6 mm. longis anthesi subglobosis ca. 0.6 mm. longis; ovarium anthesi subglobosum ca. 1 mm. longum stylo subaequale, stylo vix divisio quam antheris breviore. Capsulae maturae non visae. Fig. 11B (Holotype).

MEXICO: OAXACA: de Almoloya à Sta. Catarina, 1000 m., *C. Conzatti 1688*. HOLOTYPE MO; isotype US.

Known only from the type collection.

33. DRYMARIA MALACHIOIDES Briq. in Ann. Cons. & Jard. Bot. Gen. 13:372. 1911. (HOLOTYPE: *Galeotti 4415*; Mexicum: Cordillère d'Ario, 4000′; G!; isotype at P!)

Clambering or ascending herbaceous annuals to as much as 45 cm. high, the internodes longer than the leaves, villose with jointed hairs to as much as 1 mm. long. Leaves opposite, the blades reniform to deltoid-ovate, 1–3 cm. long, 1–3 cm. broad, apically rounded, marginally entire, obtuse to cordate basally, weakly

Fig. 11: A. *D. multiflora* (isotype); petal, 7½×; sepal, 7½×; seed, 15×. B. *D. conzattii* (holotype); portion of plant, ½×; petal, 6×; sepal, 6×. C. *D. malachioides* (holotype); flower, 7½×; petal, 6×; sepal, 6×. D. *D. villosa* (holotype of *D. barrancae*); petal, 10×; sepal 10×; seed, 20×. E. *D. villosa* (isotype of *D. hirsuta*); portion of plant, 1½×; petal, 10×; sepal, 10×; seed, 20×.

5-nerved, scantily villose; petioles 1–20 mm. long, the stipules entire or bifid, the divisions lanceolate to filiform, 1–2 mm. long. Inflorescences of terminal 3–many-flowered cymes, ultimately lax, the peduncles 1–6 cm. long; bracts 1.5–2.5 mm. long, the villose pedicels to as much as 12 mm. long. Sepals 5, 4.5–5.0 mm. long, 1.5–2.0 mm. broad, elliptic, apically acute, obscurely 3-nerved, with a few sessile glands; petals 5, 5–6 mm. long, bifid about two-thirds their length, the lobes spatulate, apically rounded to apiculate, several-nerved, basally provided with 4–6 ciliate auricles; stamens 5, 2–4 mm. long, the oblong anthers 0.5–0.8 mm. long; ovary at anthesis ovoid, the styles longer than the ovary, trifid about half their length. Capsule ellipsoid, ca. 4 mm. long, several-seeded, the seeds ca. 0.6 mm. broad, cochleate, tuberculate, the dorsal tubercles filiform, the facial substellate. Fig. 11C (Holotype).

Known only from the type collection, probably in Michoacan, and a few other collections near Tancítaro, Michoacan.

Certain characteristics of the plant suggest that it might have been derived from *D. villosa*, perhaps through polyploidy, since most of the plant parts are proportionately larger than their equivalents in *D. villosa*.

34a. Drymaria villosa subsp. villosa

Drymaria villosa Cham. & Schlecht. in Linnaea 5:232. 1830. (holotype: *Schiede & Deppe 505*; in aquosis prope Jalapam, B, probably destroyed; isotype at LE!)
Drymaria hirsuta Bartl. in Presl, Rel. Haenk. 2:8. 1831. (holotype: *Haenke s. n.* Habitat in Peruviae montanis huanoccensibus, PR!)
Drymaria cubensis Regel, in Otto & Dietr. Allg. Garten. 8:298. 1840. (No type indicated; horticultural)
Drymaria ciliaris Hort. Berol. ex C. A. Mey. in Ind. Sem. Hort. Petrop. 9:71. 1843. (Hort.; no type indicated)
Drymaria ciliata Hort. Berol. ex C. A. Mey. loc. cit. 9:71. 1843. (Hort.; no type indicated)
Drymaria cordata var. *pilosa* Schlecht. in Linnaea 26:374. 1853. (no type indicated)
Drymaria cordata var. *δ villosa* (Cham. & Schlecht.) Rohrb. in Mart. Fl. Bras. 14^2:260. 1872.
Drymaria stylosa Backer, in Bull. Jard. Bot. Buitenz. 2^{12}:15. 1913. (no type indicated)
Drymaria tepicana M. E. Jones, in Contr. West. Bot. 15:124. 1929. (holotype: *M. E. Jones 22847*; Tepic, Nayarit, POM, !)
Drymaria barrancae M. E. Jones, loc. cit. 18:65. 1931. (holotype: *M. E. Jones 27051a*; La Barranca, Guadalajara, POM!)

Prostrate or ascending annuals to as much as 45 cm. long, the internodes mostly longer than the leaves, villose to hirsute with septate hairs to as much as 2 mm. long. Leaves opposite, the blades scantily to densely villose or hirsute with cinereous or ochraceous hairs, orbicular to reniform, apically rounded to acute and apiculate, basally cordate to truncate, weakly 3–7-veined, 5–15 mm. long, 5–15 mm. broad; petioles 1–10 mm. long, the stipules mostly entire, 0.5–1.5 mm. long, scarcely distinguishable from the indument. Inflorescences of terminal and axillary 5–many-flowered cymes, the ultimate branches often tending to be racemose; peduncles 1–5 cm. long; bracts 0.5–1.5 mm. long, the pedicels 2–20 mm. long, villose. Sepals 5, 2.0–3.6 mm. long, 1–2 mm. broad, narrowly to broadly ovate or elliptic, apically acute to obtuse, villose, occasionally glabrescent, weakly

3-nerved, with translucent borders; petals 5 [absent or drastically reduced in *D. villosa* forma **tepicana** (M. E. Jones) J. Duke com. & stat. nov.], 2.0–3.6 mm. long, bifid for half their length or more, the lobes apically acute to deeply emarginate, 4-nerved, basally provided with caducous filiform auricles, these variable in number and orientation; stamens usually 5, 2.0–3.5 mm. long, the oblong anthers 0.3–0.5 mm. long, the filaments shallowly connate, devoid of staminodia; ovary at anthesis ovoid to globose, the style 1.0–1.5 mm. long, trifid to as much as half its length. Capsules ovoid to ellipsoid, 2.0–3.5 mm. long, equaling or exceeding the sepals, many-seeded (rarely as few as two in *D. barrancae*), the seeds cochleate, 0.5–0.9 mm. broad, tuberculate, the dorsal tubercles cylindric to capitate, the facial tubercles stellate. Fig. 11D (Holotype of *D. barrancae*); Fig. 11E (Isotype of *D. hirsuta*).

Central Mexico through Central America along the western coast of South America to Peru; apparently introduced and rather widespread in the East Indies.

Examination of adequate material from Mexico, type locality of *D. villosa*, from Peru, type locality of *D. hirsuta*, and from Java, type locality of *D. stylosa*, clearly shows that these are conspecific. Indonesian material is marked although inconstantly, by glabrous sepals and hirsute indument, in contrast to Mexican material, which is predominantly villose.

I have seen no specimen representing this species from the West Indies, and believe very strongly that the epithet *cubensis* results from error or misconception. The contention seems to be supported by the following quote (from Ind. Sem. Hort. Petrop. 9:71. 1843): "1093. DRYMARIA CILIATA. Eadem planta, jam diu sub *D. ciliaris* et *D. ciliatae* H. Berol. nomine culta, nunc sub nomine *D. cubensis* H. Berol. in hort. occurit. Num sit *D. cubensis* species a *D. ciliata* distincta? Ignoramus. — Nostra planta *D. villosae* est proxima et vix nisi pilis in caule et foliis rarioribus ad illa differt. M." I have seen numerous horticultural specimens under these names from various European herbaria and they were all referable to *D. villosa*.

36b. DRYMARIA VILLOSA ssp. **palustris** (Cham. & Schlecht.) J. Duke comb. & stat. nov.

Drymaria palustris Cham. & Schlecht. in Linnaea 5:232. 1830. (HOLOTYPE: *Schiede & Deppe 504*; in paludosis prope Jalapam, B, probably destroyed; Lectotype *Schiede & Deppe 405*, LE!)

Drymaria pauciflora Bartl. in Presl, Rel. Haenk. 2:8. 1831. (HOLOTYPE: *Haenke s. n.*; Habitat in Peruviae montanis huanoccensibus; PR!)

Drymaria cordata var. *β palustris* (Cham. & Schlecht.) Rohrb. in Mart. Fl. Bras. 14^2:260. 1872.

Drymaria townsendii Robinson, in Bot. Gaz. 30:58. 1900. (HOLOTYPE: *Townsend & Barber 231*; on the Sierra Madre 8 km. southeast of Colonia Garcia, Chihuahua, GH!; isotypes at F, MO, US, etc.)

Drymaria nummularia Briq. in Ann. Conserv. & Jard. Bot. Gen. 13:371. 1911. (HOLOTYPE: *Galeotti 4416*; Mexicum: Cordillere d'Ario, 4000′, G!; isotype at K).

Drymaria subsessilis M. E. Jones, in Contr. West. Bot. 15:125. 1929. (HOLOTYPE: *M. E. Jones 22848*; in rivulets at Ixtlan, Nayarit, POM!)

Drymaria sphagnophila Baehni & MacBride, in Field Mus. Bot. 13^2:625. 1937. (HOLOTYPE: *MacBride 1542*; sunny sphagnum bog, Mito, Huánuco, Peru; F!)

Prostrate annuals or erect perennials (in var. *perennis* J. Duke var. nov.*) shorter to longer than the leaves, glabrous, glandular, or rarely villose and glabrescent, the prostrate forms often rooting at the nodes, the erect forms tending to become suffrutescent. Leaves opposite, the blades 2–15 mm. long, 2–15 mm. broad, deltoid-ovate to reniform, apically rounded to apiculate, marginally entire, basally obtuse to cordate, glabrous, glandular, or villose and usually glabrescent, weakly 3–7-nerved; petioles 0.5–6.0 mm. long, the stipules entire, (rarely lacerate in var. *perennis*) filiform to lance-deltoid, 0.5–2.0 mm. long. Inflorescences of terminal and axillary 1–many-flowered cymes, the peduncles 0–10 cm. long; bracts ovate, to elliptic, acute to obtuse, 0.5–2.0 mm. long, the pedicels glabrous, rarely glandular or villosulous, 1–15 mm. long. Sepals 5, 1.0–3.0 mm. long, 1–2 mm. broad, glabrous or with sessile glands, oblong to orbicular, apically obtuse and often cucullate, very obscurely trinerved, the midrib subapically dissipating, often distally saccate; petals 5 [absent in subsp. palustris forma **townsendii** (Robinson) J. Duke comb. & stat. nov.], 1–4 mm. long, bifid from half to nearly all their length, the lobes oblanceolate to oblong, apically acute to emarginate, 1–2-nerved, the shallowly cleft petals exauriculate or with mere dentations, the deeply cleft petals usually with ciliate, downwardly directed auricles; stamens 2–5, 1.0–2.5 mm. long, the oblong to suborbicular anthers 0.2–0.4 mm. long; ovary at anthesis ovoid to globose, the styles 1.0–1.5 mm. long, bifid or trifid half their length or more, usually at least as long as the ovary. Capsule 2.0–3.5 mm. long, usually exceeding the sepals, occasionally twice as long, 5–24-seeded, the seeds cochleate, 0.6–1.1 mm. broad, densely tuberculate, the dorsal tubercles longer than broad, occasionally capitate, the facial tubercles usually stellate. Fig. 12A (Holotype of *D. villosa* ssp. *palustris* var. *perennis*); Fig. 12B (Isotype of *D. nummularia*); Fig. 12C (Isotype of *D. pauciflora*); Fig. 12D (Holotype of *D. sphagnophila*); Fig. 12E (Holotype of *D. townsendii*); Fig. 12F (Holotype of *D. subsessilis*).

Mexico through Central America at high altitudes down western South America to Peru. Bolivia.

Three rather easily discernible elements may be distinguished in this subspecies. Firstly, there is typical ssp. *palustris*, which (if I am correct in assuming that *Schiede & Deppe 405* at Leningrad is the same as *Schiede & Deppe 504*, the holotype) has large petals cleft nearly to the base and provided with ciliate auricles. This is an annual plant, usually prostrate and often rooting at the nodes. I have seen no specimens from outside Mexico. Among Mexican specimens of this element are M. E. *Jones 22848*, *Bell & Duke 16624*, *Rose & Hay 4800*, *H. E. Moore 2801*, *Hinton et al. 12233*, and *J. H. Maysilles 7782*.

By far the most common element is that prostrate form whose petals are not so deeply cleft and not so ornate, i.e. there are no ciliate auricles. In habit this is similar to the typical form and no other characters are discernably correlated.

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*D. VILLOSA ssp. PALUSTRIS var. **perennis** J. Duke var. nov. Subspecie typica differt habitu erecto perenne, sepalis quoque angusto-ovatis vel oblongis saepe glandulosis apice lividis cucullatisque, petalis dimidio fissis exauriculatis vel subexauriculatis. HOLOTYPE: *Palmer 187*; Alvarez, San Luis Potosí, Mexico, MO.

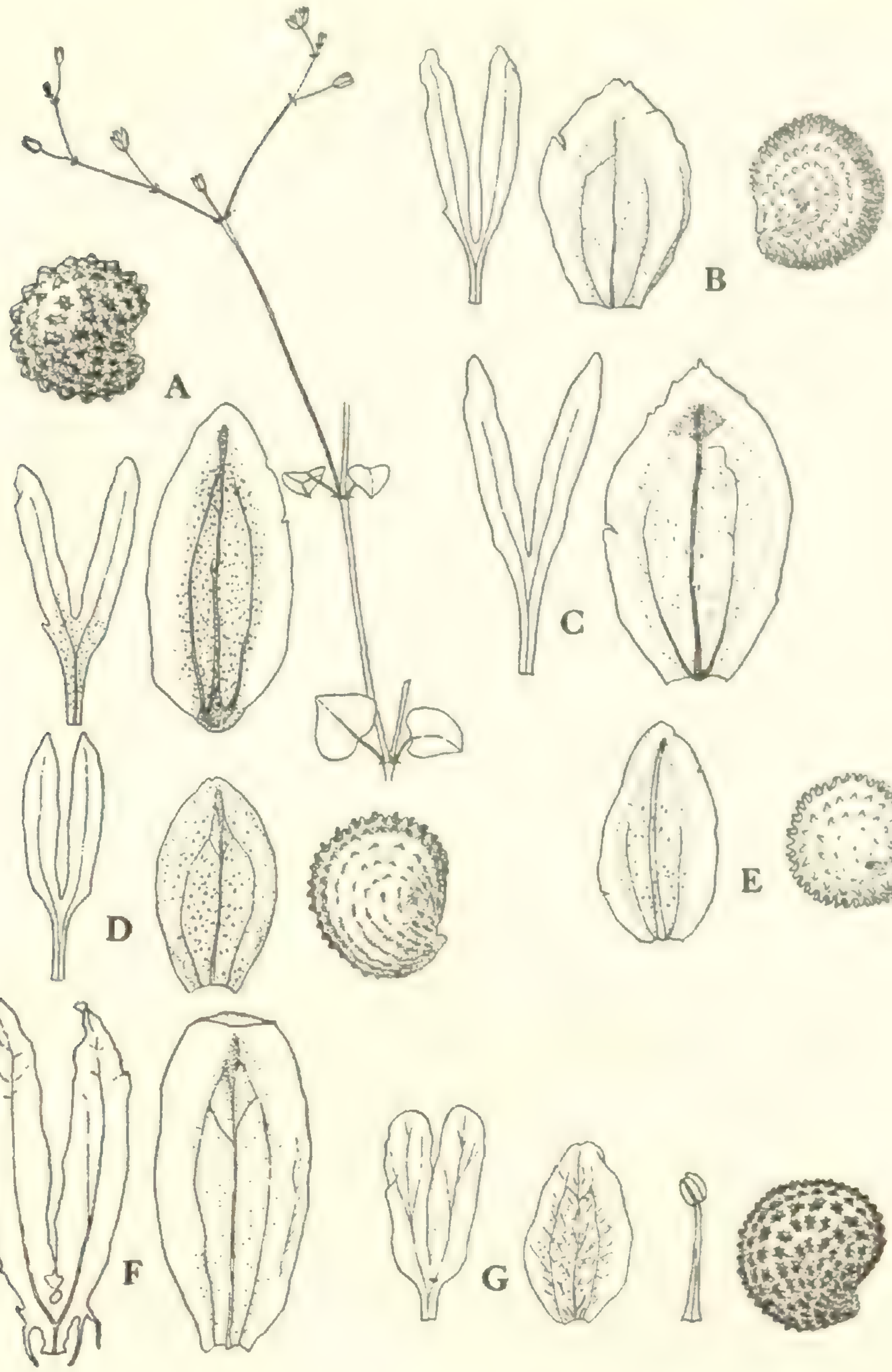

Fig. 12: A. *D. villosa* ssp. *palustris* var. *perennis* (holotype); seed, 20×; petal, 12½×; sepal, 12½×; portion of plant, ¾×. B. *D. villosa* ssp. *palustris* (isotype of *D. nummularia*); petal, 10×; sepal, 10×; seed, 20×. C. *D. villosa* ssp. *palustris* (isotype of *D. pauciflora*); petal, 15×; sepal, 15×. D. *D. villosa* ssp. *palustris* (holotype of *D. sphagnophila*); petal, 10×; sepal, 10×; seed, 20×. E. *D. villosa* ssp. *palustris* forma *townsendii* (holotype); sepal, 10×; seed, 15×. F. *D. villosa* ssp. *palustris* (holotype of *D. subsessilis*); petal, 15×; sepal, 15×. G. *D. villosa* ssp. *paramorum* (holotype except seed); petal, 5×; sepal, 5×; stamen, 5×; seed, 20×.

To this more prevalent portion of the population, the following names have been applied: *D. pauciflora, D. nummularia, D. sphagnophila.*

The third element seems to have received no name previously. To this belong erect perennial relatives which have little else in the way of differentia, except a more pronounced tendency to have subacute, somewhat cucullate sepals and glandular herbage. Representing specimens of the var. *perennis*, which may have resulted from gene exchange with *D. laxiflora* or one of its relatives, are *Palmer 356*, and *187, Pringle 3265, I. M. Johnston 8965, M. T. Edwards 804B, H. E. Moore 1669,* and *Salinas, Rowell & Barkley 16M375.*

In Ecuador where the plants are considered medicinal, this, the "Drimaria llamba" is reputed to be the most potently therapeutic of the local species.

34c. Drymaria villosa subsp. **paramorum** (S. F. Blake) J. Duke comb. & stat. **nov.**

Drymaria paramorum S. F. Blake, in Contr. U. S. Nat. Herb. 20:521. 1924. (HOLOTYPE: *A. Jahn 111*; Paramo de la Cristalina, Trujillo, Venez.; alt. 2900 m.; US!)

Prostrate or ascending annuals to as much as 20 cm. long, the internodes mostly longer than the leaves, sparsely to densely villose with caducous septate hairs. Leaves opposite, the blades 5–10 mm. long, 4–8 mm. broad, broadly ovate, apically acutish, basally rounded to cordate, trinerved, sparsely to densely villose; petioles 0.5–3.0 mm. long, the stipules entire, scariose, lance-deltoid, ca. 1 mm. long. Inflorescences of lax 3–many-flowered cymes, the glabrous to villose peduncles to 4 cm. long; bracts scariose, ovate, acute, mucronulate, 1.0–2.5 mm. long, the glabrous to villose pedicels 2–6 mm. long. Sepals 4–5, subequal, 3.5–4.2 mm. long, 1.2–2.0 mm. broad, the outer villose, broadly oblong, obtuse, weakly trinerved, marginally scariose, the inner glabrous, almost nerveless, broader; petals 4–5, 3.5–5.0, bifid about half their length, the lobes oblong, 3–7-nerved, obtuse, exauriculate or with minute deltoid auricles at the base, tapered abruptly to the linear claw; stamens 4–5, 2–3 mm. long, the oblong anthers ca. 0.5 mm. long; ovary at anthesis subglobose, the style trifid about half its length, slightly exceeded by the anthers. Capsule equaling or exceeding the sepals, ca. 3.5 mm. long, 15–34-seeded, the seeds 0.8–1.2 mm. broad, tuberculate, the tubercles stellate. Fig. 12G (Holotype; [seed from *Pittier 13170*]).

Trujillo and Merida, Venezuela; also from the Cordillera Oriental in Colombia.

Certain specimens of *D. ovata* from Ecuador (e.g. *Fosberg & Giles 23225* and *Rose & Rose 23225*) seem to share some of the characteristics of this subspecies.

O. Series GRANDIFLORES

Leaves opposite, ovate to reniform, sessile or petiolate, entire or crenulate, stipulate, the stipules entire or lacerate. Flowers in lax or subcapitate terminal or axillary many-flowered cymes. Sepals acute or obtuse, weakly to strongly 3–7-nerved, the midrib often carinate. Petals bifid (absent in *D. apetala*), unguiculate (subexunguiculate in *D. glaberimma*), exauriculate or with deltoid auricles, the lobes 2–15-nerved. Stamens 5. Seeds cochleate, tuberculate (smooth in forms of *D. ovata*), the tubercles domical or conical, not stellate nor capitate nor cylindric.

8 species from Colombia to Argentina, along western South America. Figs. 13 and 14.

a. Seeds lustrous, smooth to tuberculate; flowers at anthesis obconical; petals about equaling the sepals, bifid ca. half their length, exauriculate.
  b. Seeds tuberculate; leaves glabrous and pergameneous, the stipules ca. as long the the petioles; Venezuela.....35. D. FIRMULA
  b. Seeds smooth to corrugated; leaves glabrous to villose, membranaceous to pergameneous, the petioles usually longer than the stipules; Colombia to Argentina.....36. D. OVATA
a. Seeds not lustrous, variously tuberculate; flowers at anthesis usually pyriform; petals minute to twice as long as the sepals, bifid one-half to three-fourths their length, occasionally auriculate.
  c. Petals vestigial or absent; sepals 6–10 mm. long.....37. D. APETALA
  c. Petals present and obvious; sepals 2.5–8.0 mm. long.
    d. Sepals acute, glabrous; inflorescences often long-pedunculate in the leaf axils; petals occasionally subexunguiculate, the lobes oblong.
      e. Tubercles of the seeds secondarily tuberculate; trunk of the petal longer than the claw; Peru.....38. D. GLABERRIMA
      e. Tubercles of the seeds simple; trunk of the petals shorter than the claw; Galapagos Islands.....39. D. MONTICOLA
    d. Sepals acute to obtuse, if acute, carinate or glandular; inflorescences terminal; petals unguiculate, the lobes oblong to narrowly obovate:
      f. Petals 6–15 mm. long, the lobes oblong, tapered to the claw; leaves elliptic to ovate, glabrous to villose, often strongly crenulate; tubercles of the seeds obtuse;
        g. Sepals more or less obtuse, shorter than the petals, not carinate, often glandular or villose; leaves not crenulate; alpine Peru.....40. D. GRANDIFLORA
        g. Sepals acute, about as long as the petals, the outer carinate, the carinae often serrulate; leaves often crenulate; lomas of Peru.....41c. D. PAPOSANA var. SERRULATA
      f. Petals less than 6 mm. long, if rarely that long, with narrowly ovate lobes, truncate to the claw; leaves ovate, glabrous to glandular, not crenulate; tubercles of the seeds often acute:
        h. Sepals acute, carinate, 4.0–6.5 mm. long, usually glandular; loma plants of Peru and Chile:
          i. Petal-lobes narrowly obovate, truncate to the claw, conspicuously exserted; inflorescence capitate; Peru.....41b. D. PAPOSANA var. WEBERBAUERI
          i. Petal-lobes oblong, tapered to the claw, slightly if at all exserted; inflorescence capitate to cymose; Chile.....41a. D. PAPOSANA var. PAPOSANA
        h. Sepals obtuse to acute, if carinate, then obtuse, 2.5–5.0 mm. long, glabrous or slightly glandular; Peru and the Galapagos Islands, Ecuador and Bolivia:
          j. Sepals ellipsoid to orbicular, very obtuse, occasionally slightly glandular.....42a. D. ROTUNDIFOLIA var. ROTUNDIFOLIA
          j. Sepals narrowly to broadly ovate, acutish, glabrous, often carinate.....42b. D. ROTUNDIFOLIA var. NITIDA

35. DRYMARIA FIRMULA Steyermark, in Field Mus. Bot. 28[1]:227. 1951. (HOLOTYPE: *Steyermark 56536*; Venezuela; Merida; Páramo de los Colorados, between El Molino & San Isidro Alto, 2745–2955 m. F!)

Ascending or erect herbs to as much as 25 cm. high, the internodes mostly longer than the leaves, often cyanic. Leaves opposite, the blades glabrous, subpergameneous, 3.0–8.5 mm. long, 2.5–7.0 mm., apically acute, marginally involute, basally cordate, subsessile or on petioles to 1.5 mm. long, the stipules lacerate, the divisions linear, caducous, equaling or exceeding the petioles. Inflorescences of lax terminal 3–7-flowered cymes, the axes glabrous to minutely glandular; bracts ovate, 1-nerved, scariose, 1.5–2.5 mm. long, mostly equaling or exceeding the subtended pedicels. Sepals 5, subequal, glabrous, 3.8–4.8 mm. long, 1.4–2.0 mm.,

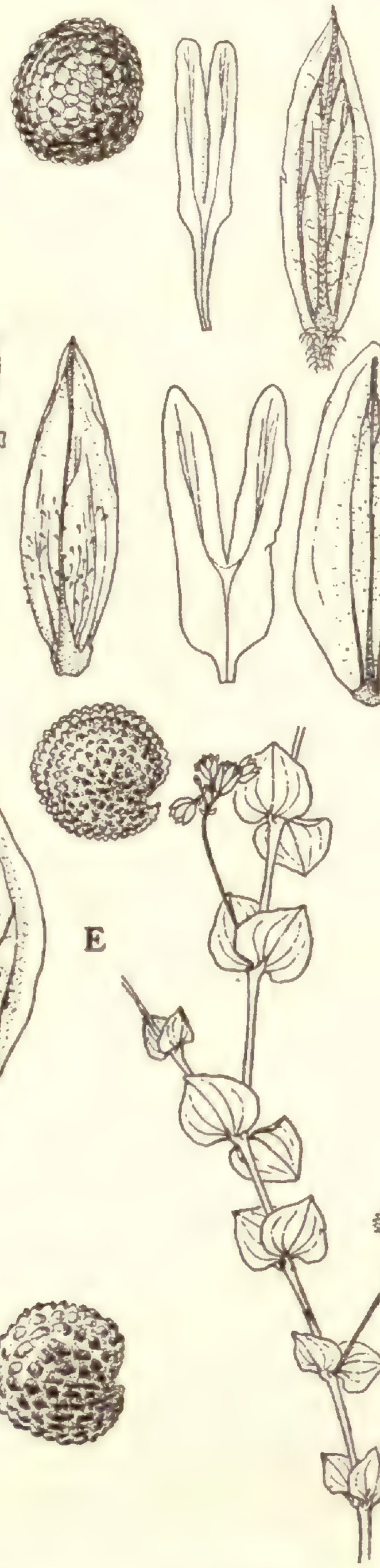

Fig. 13: A. *D. firmula* (holotype); petal, 6×; sepal, 6×; stamen, 6×; seed, 17½×. B. *D. ovata*; petal, 6×; sepal, 6×; seed, 15×. C. *D. apetala*; androecium, 7½×; "petal", ca. 20×; seed, 15×; sepal, 5×. D. *D. glaberrima* (isotype); petal, 7½×; sepals, 7½×; seed, 20×; tubercles of seed, ca. 60×. E. *D. monticola* (holotype); petal, 5×; sepals, 5×; seed, 15×; portion of plant, ½×. F. *D. grandiflora*; petal, 3×; sepal, 3×; seed, 10×.

narrowly ovate to oblong, obtuse, trinerved, the midrib of the outer, somewhat narrower, sepals often excurrent; petals 5, 4.5–5.0 mm. long, bifid slightly more than half their length, the lobes broadly oblong, obtuse, 1–4-nerved, ca. 1 mm. broad, gradually tapered to the claw, exappendiculate or unidentate; stamens 5, 3.0–3.5 mm. long, the oblong anthers ca. 0.6 mm. long; ovary at anthesis ellipsoid, the long style trifid for about one-third its length, about attaining the apex of the sepals. Capsule ovoid, 3-valved, 2 mm. long, 2-seeded, the seed cochleate, 1.2–1.5 mm. broad, dorsally tuberculate, the tubercles low and domical, facially merely reticulate, sublustrous. Fig. 13A (Holotype).

Known only from the type collection.

The lacerate stipules, small domical tubercles on the large seeds and the occasionally 1-nerved petal-lobes suggest a close affinity with *D. cordata*. On the other hand, the size and shape of the petals, coupled with the subsessile, subpergameneous leaves, suggest a closer alliance with *D. ovata*, *D. monticola* and *D. glaberrima*, and these four poorly known species seem to form a closely knit group.

36. Drymaria ovata Humb. & Bonpl. ex Roem. & Schultes, Syst. Veg. 5:406. 1819. (holotype: *Humb. & Bonpl. s. n.*: crescit prope Quito, alt. 1460 hex. *n. v.*)

Prostrate to rigidly ascending annuals or perennials to as much as 50 cm. high, the internodes mostly longer than the leaves, glabrous, farinose, glandular-puberulent or densely villose. Leaves opposite, the blades glabrous to villose, membranaceous to subpergameneous, deltoid-ovate to reniform, apically acute and apiculate to rounded, basally truncate to subcordate, 5–40 mm. long, 5–30 mm. broad, subsessile or the petioles to as much as 8 mm. long, the stipules mostly lacerate, the divisions filiform to lanceolate. Flowers broadly obconic, 1–many in lax terminal, rarely axillary, cymes, the peduncles to as much as 12 cm. long; bracts lanceolate, 2–5 mm. long, usually shorter than the glabrous to villose pedicels. Sepals 5, glabrous to villose, elliptic to ovate, 4.0–6.5 mm. long, apically acute to obtuse, marginally entire, 3–8-nerved, the inner broader, more obtuse and glabrous; petals 5, 4–7 mm. long, bifid one-half to three-fourths their length, the lobes narrowly oblong, 2–5-nerved, apically obtuse or emarginate, basally truncate or rarely tapered to the narrow claw, usually exappendiculate; stamens 5 (–6), the oblong anthers 0.4–1.0 mm., the filaments 2–5 mm. long; ovary at anthesis ovoid, the style 1–2 mm. long, bifid or trifid about half its length. Capsules 2.0–4.5 mm. long, 2–15-seeded, the seeds tightly circinnate, subdiscoid, 0.9–1.5 mm. broad, smooth or provided with low domical tubercles, often nearly black, lustrous. Fig. 13B (*Lehmann 6112*).

Along the Andes from Venezuela to northern Argentina.

Exhibiting a confusing array of variation, this polymorphic species is difficult of definition, but a rather constant correlation of flower- and petal-shape seems to prevail. The lustre of the seeds, equaled nowhere else in the genus, is usually evident, even in those forms which have tuberculate seeds. The following contrasting characteristics may be found in representative specimens: ovate vs. reni-

form leaves, sessile vs. petiolate leaves, membranaceous vs. subpergameneous leaves, petals tapered vs. truncate to the claw, and smooth vs. tuberculate seeds. With this number of variables, and undoubtedly more exist, many combinations are possible, and I have seen many of them, but am unable to detect any correlations among these characteristics except that, south of Peru, all specimens have had smooth seeds and large leaves. *Weberbauer 6543* from Peru differs in having subpergameneous leaves, 1–2-nerved petal-lobes, and a farinose girdle on the pedicels, characteristics suggesting that it might have resulted from hybridization with *D. cordata*. From Huanuco, *Macbride & Featherstone 1714* has most of the features of *D. cordata* but the seeds are nearly smooth and lustrous, and the veins in the petal-lobes have several branches.

Collections made by Prieto for W. W. Camp in Prov. Cañar and Azuay of Ecuador possessed the colloquial names "Drimaria del cerco" and "Drimaria macho" and the plants are utilized as treatments for liver and kidney ailments.

37. Drymaria apetala Bartl. in Presl, Rel. Haenk. 2:7. 1831. (holotype: *Haenke s. n.* Habitat in Chile; PR!)

Stellaria virgata Seringe, in DC. Prodr. 1:396. 1824. not *D. virgata* Briq., 1911. (holotype: patr. ign. "Alsine virgata Deless. herb.": G, *n. v.*)
Drymaria macrantha A. Gray, Bot. U. S. Expl. Exped. 126. 1854. (holotype: *Wilkes exped. s. n.*; Obrajillo; US!)
Drymaria virgata Briq. in Ann. Cons. & Jard. Bot. 13:370. 1911.

Virgate or sparingly branched suffrutescent perennials (?) to as much as 30 cm. high, the internodes mostly longer than the leaves, locally farinose. Leaves opposite, the blades glabrous to minutely glandular, narrowly to broadly ovate, apically acute, basally cordate and somewhat clasping, 5–15 mm. long, 3–9 mm. broad; stipules mostly entire, deltoid, acuminate, caducous, 0.5–1.5 mm. long. Inflorescences of rather dense few-flowered cymes, the axes often densely glandular; bracts lanceolate, acuminate, strongly 1-ribbed, 2.5–4.0 mm. long; pedicels 2–10 mm. long. Sepals 5, subequal, rather densely glandular, 7.5–9.0 mm. long, narrowly ovate, apically acute with the midrib often excurrent as an apiculum, basally rather strongly trinerved; petals 5, reduced to mere vestiges or completely absent; stamens 5, 5.5–6.5 mm. long, the oblong anthers 1.8–2.0 mm. long; ovary at anthesis narrowly ellipsoid, the trifid style exceeded by the anthers. Capsule included, 5.5–6.5 mm. long, many-seeded, the submature seeds cochleate, rather sharply pointed at the hypocotylar end, dorsally sulcate, weakly tuberculate, the tubercles low and subhemispherical. Fig. 13C.

Although attributed to Mexico, erroneously, and questionably to Chile, I have seen no specimens that were collected outside of Peru. The Pavon specimens from "Mexique" and from Peru, probably are duplicates of one collection.

38. Drymaria glaberrima Bartl. in Presl, Rel. Haenk. 2:7. 1831. (holotype: *Haenke s. n.*; habitat in Peruviae montanis huanoccensibus; PR!; isotype at GOET)

Procumbent or ascending lignescent annuals or perennials to as much at 45 cm. high, the internodes mostly longer than the leaves. Leaves opposite, the blades

glabrous, narrowly to broadly ovate or elliptic, apically acute, marginally entire or undulate, basally obtuse to truncate, 3–5-nerved, subsessile, the stipules filiform, caducous, usually exceeding the petioles. Inflorescences of mostly axillary 3–11 flowered cymes, the peduncles 1–8 cm. long; bracts lanceolate to ovate, 1.5–2.5 mm., all except those of the central flowers equaling or exceeding the glabrous subtended pedicels. Sepals 5, glabrous, narrowly ovate, apically acute to obtuse, weakly 3–5-nerved, 4.0–5.0 mm. long, the inner obtuse, with a broad hyaline margin, ca. 2 mm. broad; petals 5, 3.0–4.5 mm. long, bifid halfway or slightly more, the lobes oblong, obtuse, 3–7-nerved, ca. 0.5 mm. broad, the trunk ca. 1 mm. broad, truncate to a minute claw, or completely exunguiculate; stamens 5, ca. 3 mm. long, the oblong anthers ca. 0.6 mm. long, the filaments basally connate into a very shallow cup; ovary broadly oblongoid, the style ca. 1.5 mm. long, trifid ca. half its length. Capsule oblongoid, 2–10-seeded, the seeds tightly circinnate, tuberculate, the dorsal tubercles longer than broad, often themselves secondarily tubercululate, the facial tubercles low and domical or slightly elongated. Fig. 13D (Isotype).

Known from several stations, all in Peru.

The material that I am citing for this species is heterogeneous indeed and it is possible that more than one taxon is involved. Intensive collecting and field studies will be needed to clarify this whole series, which is still full of problems.

39 DRYMARIA MONTICOLA Howell in Proc. Cal. Acad. 421:329. 1935. (HOLOTYPE: *J. T. Howell 9243*; Mt. Crocker, Indefatigable Island; CAS!)

Decumbent or ascending perennials, to as much as 40 cm. high, the glabrous internodes exceeding the leaves, the roots to 4 mm. thick. Leaves opposite, the blades glabrous, 3–5-nerved, ovate, acute, marginally undulate, basally truncate to subcordate, subsessile; the stipules mostly bifid, 1–2 mm. long, exceeding the petioles. Flowers in rather dense 5–9-flowered cymes, the peduncles 2–7 mm. long, glabrous, the bracts ovate, 1.0–1.5 mm. long, shorter or slightly longer than the glabrous pedicels. Sepals 4–5, glabrous, narrowly to broadly ovate, weakly 3-ribbed 4.5–6.0 mm. long, 1.5–2.5 mm. broad, apically acute, the midrib subapically dissipating, the lateral ribs weak, with 2 intercalary veins; petals 4–5, 4–5 mm. long, bifid about half their length, the lobes oblong, obtuse, 2–4-nerved, often basally auriculate, tapered to the linear claw; stamens 4–5, 3.5–4.5 mm. long, the oblong anthers 0.7–0.9 mm. long, the filaments basally connate into a cup to as much as 0.7 mm. deep; ovary globose to ovoid, stipitate, the styles 1.5–2.0 mm. long, trifid a little more than half their length. Capsule 2.0–3.5 mm. long, 8–16-seeded, the seeds tightly cochleate, ca. 1 mm. broad, tuberculate, the dorsal tubercles domical, slightly higher than broad, grading into the polygonal facial tubercles. Fig. 13E (Holotype).

Known only from the Galapagos Islands.

This species was likened by its author to *D. apetala* (*D. macrantha*) and in its sessile leaves it does somewhat resemble that species. A closer relative appears to be *D. firmula* from Venezuela which differs somewhat in its strongly three-ribbed sepals and exappendiculate petals. *D. glaberrima* also belongs in this relationship but differs in its tuberculate tubercles and obtuse inner sepals.

40. Drymaria grandiflora Bartl. in Presl, Rel. Haenk. 2:7. 1831. (holotype: *Haenke s. n.* Habitat in Chile, et in Peruviae montanis huanoccensibus; PR!)

Prostrate or clambering rarely ascending perennials, the internodes mostly longer than the leaves, villose to glabrescent. Leaves opposite, the blades glandular-villosulous, rarely glabrous, narrowly to broadly ovate, weakly to strongly 3-nerved, apically acute, marginally entire, basally rounded to truncate, usually clasping; the main leaves 10–30 mm. long and 5–20 mm. broad, those of the branches much smaller; stipules entire to lacerate 1.0–2.5 mm. long, usually longer than the petioles. Flowers narrowly to broadly campanulate in terminal, lax, few-flowered cymes, the peduncles 1–15 cm. long; bracts 2–5 mm. long, usually much exceeded by the pedicels, the pedicels usually densely glandular-villosulous, 3–25 mm. long. Sepals 5, glandular-puberulent to glabrous, ovate, weakly nerved, 6–8 mm. long, the outer sometimes carinate and acute, the inner flatter and often obtuse; petals 5, 7–12 mm. long, bifid about two-thirds their length, the lobes linear to oblong, apically obtuse, many nerved, to as much as 3 mm. broad, basally gradually merging with the poorly differentiated trunk and claw, exauriculate or rarely unilaterally unidenticulate; stamens 5, the anthers oblong 1.0–1.5 mm. long, the filaments 4–6 mm. long, connate into a cup as much as 1.5 mm. deep; ovary at anthesis ellipsoid, usually longer than the style, the style 2–3 mm. long, trifid about one-third its length. Capsule ellipsoid, 4–5 mm. long, 5–many-seeded, the seeds tightly circinnate 1.2–1.6 mm. broad, coarsely tuberculate, the tubercles dorsally conical, somewhat flattened, grading facially into polygonal tubercles. Fig. 13F.

Peru; departments Huanuco, Cajamarca, and Lima; reported from Chile, but perhaps erroneously.

41a. Drymaria paposana var. paposana

Drymaria paposana Phil. Fl. Atac. 10. 1860. (holotype: *Philippi s. n.;* prope Paposo in valle Tartal alisque locis ejusdem regionis crescit, SGO? *n. v.* photograph of isotype from destroyed Austrian herbarium; MO!)

Upright or ascending annuals to as much as 25 cm. high, the internodes mostly longer than the leaves, glandular-puberulent, the taproot to as much as 2 mm. thick. Leaves opposite, the blades narrowly to broadly ovate, apically acute, basally cuneate to subcordate, glabrous or scantily glandular-puberulent, the upper leaves sessile, 5–20 mm. long, 4–18 mm. broad, the stipules lacerate, the divisions filiform, mostly exceeding the petioles. Inflorescences of terminal subcapitate or monopodial cymes, the peduncles 1–30 mm. long, glandular-puberulent, the bracts ovate, usually longer than the glandular pedicels. Sepals 5, 3.5–5.0 mm. long, ellipsoid, glandular to glabrous, apically obtuse, weakly 3-nerved, the midrib subapically dissipating, the outermost sepals occasionally carinate; petals 5, 3.5–4.5 mm. long, bifid about half their length, the lobes oblong, rarely to 1 mm. broad, apically obtuse or emarginate, 2–3-nerved, tapered gently to the claw, exauriculate; stamens 5, 2.7–3.0 mm. long, the oblong anthers ca. 0.6 mm. long; ovary at anthesis ovoid, the style ca. 1.2 mm. long, trifid about half its length. Capsules 2.6–3.0 mm. long, many-seeded, the seeds cochleate, 0.6–0.8 mm. broad, the tubercles conical, acute. Fig. 14D.

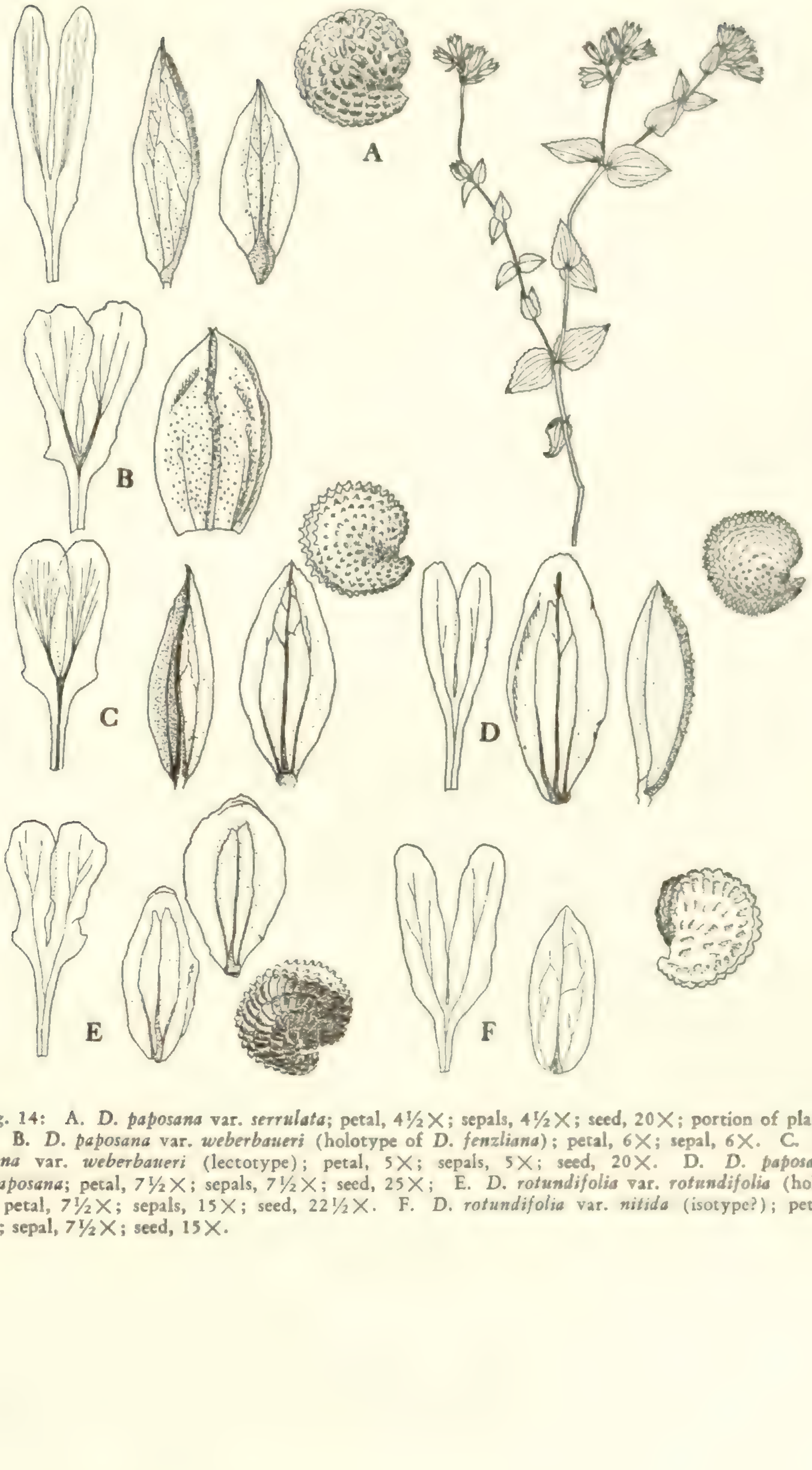

Fig. 14: A. *D. paposana* var. *serrulata*; petal, 4½×; sepals, 4½×; seed, 20×; portion of plant, ½×. B. *D. paposana* var. *weberbaueri* (holotype of *D. fenzliana*); petal, 6×; sepal, 6×. C. *D. paposana* var. *weberbaueri* (lectotype); petal, 5×; sepals, 5×; seed, 20×. D. *D. paposana* var. *paposana*; petal, 7½×; sepals, 7½×; seed, 25×; E. *D. rotundifolia* var. *rotundifolia* (holotype) petal, 7½×; sepals, 15×; seed, 22½×. F. *D. rotundifolia* var. *nitida* (isotype?); petal, 7½×; sepal, 7½×; seed, 15×.

Northern Chile.

Although I. M. Johnston lumped this with *D. cordata*, it is quite distinct from that species in many respects.

41b. Drymaria paposana var. **weberbaueri** (Muschl.) J. Duke comb. & stat. nov.

Drymaria weberbaueri Muschl. in Engl. Bot. Jahrb. 45:451. July 25, 1911. (HOLOTYPE: *Weberbauer 1662*; Peru, Barranca prope Lima in formatione "Loma" dicta, 50–200 m. s. m.; B, *n. v.*, probably destroyed; as lectotype may be designated *Weberbauer 1657* at Geneva!)

Drymaria fenzliana Briq. in Ann. Cons. & Jard. Bot. Gen. 13:373. May 10, 1911. (HOLOTYPE: *Pavon s. n.*, "Mexique", G!)

Erect or ascending annuals to as much as 30 cm. tall, the few internodes mostly longer than the leaves, glabrous to glandular-pubescent. Leaves opposite, the blades glabrous to glandular-puberulent, narrowly to broadly ovate, 5–20 mm. long, 4–15 mm. broad, apically acute, basally cuneate to truncate or subcordate, usually subsessile, the lacerate stipules mostly longer than the petioles. Inflorescences of terminal, usually subcapitate, 3–many-flowered cymes, the peduncles 1–4 cm. long, the pedicels 0.5–3.0 (–5.0) mm. long, glandular-puberulent, usually exceeded by the ovate, occasionally dentate, bracts. Sepals 5, 3.5–7.0 mm. long, ovate, usually glandular, the outer acute and often carinate, 1–3-nerved, the inner often broader, more obtuse, less glandular; petals 5; 5–7 mm. long, usually exceeding the sepals, bifid little more than half their length, the lobes broadly oblong to spatulate, to 2 mm. broad, 3–many-nerved, apically obtuse or emarginate, basally auriculate, often asymmetrically so, more or less truncate to the linear claw; stamens 5, 3.0–5.0 mm. long, the oblong anthers 0.5–1.0 mm. long, the filaments shallowly connate; ovary at anthesis ovoid to ellipsoid, the style 1.0–2.5 mm. long, trifid for about one-third its length. Capsule ovoid, 3-valved, often stipitate, 2.5–4.0 mm. long, many-seeded, the seeds cochleate, 0.5–1.0 mm. broad, tuberculate, the tubercles mostly domical and obtuse. Fig. 14B (Holotype of *D. fenzliana*); Fig. 14C (lectotype of *D. weberbaueri*).

Lomas of Peru from the departments of Lima to Arequipa.

With its rather dense clover-like heads, this is perhaps the most handsome *Drymaria*. A nice photograph may be seen in Goodspeed and Stork (in Univ. Cal. Publ. Bot. 28: *pl. 8.* 1955). Although Briquet in his description of *D. fenzliana* believed it to be a Mexican species, it becomes apparent that the label on the Pavon specimen had suffered the same fate as those on some of his specimens of *D. apetala*, some of which were labeled as being from Mexico and others from Peru, although obviously belonging to the same collection.

Toward the southern end of its range, this variety intergrades with the var. *paposana* and the newly described var. *serrulata*.

41c. Drymaria paposana var. **serrulata** J. Duke var. nov.

Plantae perennes erectae vel glabrae sublignosae internodis quam foliis saepe longioribus, radice usque 1 cm. in diametro. Folio opposita laminis glabris anguste vel late ovatis apice acutis saepe mucronatisque basim tuncatis usque cordatis, saepe

marginibus conspicue crenulatis 5-nervatisque subsessilibus, stipulis laceratis quam petiolis longioribus. Flores 3 usque multi cymis terminalibus laxis aut vix confertis pedunculis 1–8 cm. longis, pedicellis minus 1 cm. longis rare divaricatis. Sepala 5, 5–8 mm. longa, 2.5–3.5 mm. lata minute granulosa angusto-ovata vel elliptica, apice acuta (externissimo carinato cum carinis saepe serrulatis); petala 5, 6–8 mm. longa, 2/3-bifida lobis oblongis 4–6-nervatis exauriculatis vel auriculatis parvis vix ungue constricto; stamina 5, 4.5–6.5 mm. longa, antheris oblongis ca. 1.5 mm. longis; ovaria ovoidea vel ellipsoidea, stylo ca. 2 mm. longo, 3/4-trifido. Capsulae inclusae seminibus multis ca. 0.8 mm. latis crasse tuberculatis opacis. Fig. 14A.

PERU: Dept. Arequipa, Prov. Caraveli; Lomas de Atiquipa (Taimara); falda arcillosa-pedregosa, 500–550 m.; *Ramon Ferreyra 13490*. (HOLOTYPE MO).

Not uncommon in the lomas from the departments of Arequipa and Moquegua, this unusual variety seems largely to replace var. *weberbaueri*, and although it resembles that variety in habit, the differences in their flowers are quite striking. Although the epithet applies to the carina of the outer sepals, the leaves themselves are often distinctively crenulate, so much so as to appear serrulate. See Fig. 14A.

42a. DRYMARIA ROTUNDIFOLIA var. ROTUNDIFOLIA

Drymaria rotundifolia A. Gray, Bot. U. S. Expl. Exped. 123. 1854. (HOLOTYPE: *Wilkes Expedition s. n.* Obrajillo, Peru US!)

Upright annuals to as much as 20 cm. high, the internodes mostly longer than the leaves, glabrous to glandular-puberulent. Leaves opposite, the blades glabrous to minutely glandular, reniform, apically rounded or apiculate, basally clasping, 4–10 mm. long, 5–15 mm. broad; the stipules lacerate, caducous. Inflorescence of rather congested 3–11-flowered cymes, the peduncles glandular, 1–45 mm. long; bracts scarious, ovate, acute, 0.5–2.0 mm. long; pedicels mostly 1.5–3.0 mm. long, those of the central flowers to 8 mm. long; glandular. Sepals 5, glabrous or sessile-glandular, broadly ellipsoid, obtuse or rounded, subcucullate, weakly 3-nerved, the midvein subapically dissipating, often carinate, marginally scarious and transparent, 2.5–3.5 mm. long, 1.2–2.8 mm. broad; petals 5, 3.2–4.5 mm. long, bifid about half their length, the lobes oblong, ca. 0.5 mm. broad, exappendiculate but somewhat flared before narrowing into the linear claw; stamens 5, about 3 mm. long, the oblong anthers about 0.6 mm. long; ovary at anthesis turbinate to ellipsoid, the style trifid about half its length, ca. 1.5 mm. long, exceeded by the anthers. Mature capsule ellipsoid, 2.5–3.5 mm. long, several-seeded, the seeds cochleate, often dorsally sulcate, 0.6–0.8 mm. broad, tuberculate, the tubercles conical, obtuse or rarely acute. Fig. 14E (Holotype).

Peru.

Stewart 1512 from the Galapagos Islands might just as well be included here as in var. *nitida*. The specimen has some of the characters of both varieties, and perhaps represents a new entity.

42b. DRYMARIA ROTUNDIFOLIA var. **nitida** (J. Ball) J. Duke comb. & stat. nov.

Drymaria nitida J. Ball, in Jour. Linn. Soc. 22:31. 1887. (HOLOTYPE: Peru: Ex saxosis Andium Peruviae juxta pagum Chicla, 12–13000′ s. m. *J. Ball s. n.* K, *n. v.*, isotype at GH!)

Minute to rather large ascending annuals to as much as 15 cm. high, the internodes glabrous, mostly longer than the leaves. Leaves opposite, the blades glabrous, often somewhat fleshy, narrowly ovate to elliptic, 3–10 mm. long, 2–8 mm. broad, glabrous, apically acute to cuspidate, marginally hyaline, basally attenuate and clasping, the venation obscure; stipules entire, very fugaceous, acicular, less than 1 mm. long. Flowers campanulate, in rather dense few-flowered terminal cymes, the lowermost bracts merging with the leaves, often stipulate, ovate, ca. 1.5 mm. long; peduncles 4–7 mm. long, the pedicels glabrous, exceeded by or slightly exceeding the bracts. Sepals 5, glabrous, 2.5–3.0 mm. long, the outer broadly oblong and weakly carinate, the inner suborbicular, obtuse, to 2 mm. broad, obscurely nerved, the midnerve often subapically dissipating; petals 5, 3.2–4.0 mm. long, bifid about two-thirds their length, the lobes narrowly spatulate, apically obtuse, 2–3-nerved, exauriculate, acutely tapered to the claw; stamens 3–5, 2.5–3.5 mm. long, the anthers oblong; ovary at anthesis cordate, ca. 8-ovulate, the style deeply trifid. Capsules subglobose, 3–8-seeded, ca. 2 mm. long, the seeds ca. 1 mm. broad, tuberculate, the tubercles subdendritic. Fig. 14F (Isotype).

Peru, Ecuador and the Galapagos Islands.

Although the type is a diminutive plant, other specimens that I refer to this variety attain a good size and in some respects approach *D. glaberrima*: e.g. *Mandon 948* from Bolivia. Characters in the flowers however suggest that it is closer allied to *D. rotundifolia* and *D. paposana*, especially its var. *weberbaueri*.

P. Series DIVARICATAE

Leaves opposite, petiolate, elliptic to reniform, stipulate. Flowers in cymes, the pedicels usually long and divaricate, exceeding the bracts. Sepals trinerved, acute, occasionally saccate basally. Petals bifid about half their length, with mamilliform auricles (except *D. divaricata* forms), the lobes (1–) 2–5-nerved. Stamens 4–5. Seeds cochleate, tuberculate, the tubercles domical conical, occasionally subdendritic or mamilliform. Five poorly defined varieties in Peru and Bolivia. Fig. 15.

a. Leaves broadly ovate to reniform, short- to long-petiolate, glabrous to villosulous; pedicels erect to strongly divaricate, mostly longer than the flowers, if shorter, viscid; sepals usually glandular or villosulous; loma or alpine plants:

b. Sepals weakly nerved, basally saccate; petals weakly auricled, the auricles deltoid when present; tubercles of seeds mamilliform or secondarily tuberculate:

c. Leaves long-petiolate; petals as long to twice as long as the sepals; seeds with mamilliform or coarsely domical tubercles.....43a. D. DIVARICATA var. DIVARICATA

c. Leaves short-petiolate; petals about as long as the sepals; seeds with the tubercles secondarily tuberculate.....43b. D. DIVARICATA var. STRICTA

b. Sepals strongly nerved, rather evenly keeled, not basally saccate; petals strongly auriculate, the auricles oblong; tubercles of the seeds domical or conical:

d. Sepals and herbage densely viscid-glandular; pedicels not divaricate; alpine plants.....43c. D. DIVARICATA var. VISCIDULA

d. Sepals and herbage subglabrous to villosulous; pedicels divaricate; loma plants.....43d. D. DIVARICATA var. DIVERGENS

a. Leaves elliptic to broadly ovate, short-petiolate, glabrous; pedicels strongly divaricating, little if any longer than the flowers, glabrous; sepals glabrous; loma plants.....43e. D. DIVARICATA var. REFLEXIFLORA

Fig. 15: A. *D. divaricata* var. *reflexiflora* (holotype); habit, ½×; petal, 7½×; sepal, 7½×; seed, 20×. B. *D. divaricata* var. *divaricata*; petal, 4×; sepals, 4×. C. *D. divaricata* var. *stricta* (isotype of *D. agapatensis*); petal, 6×; sepal, 6×; seed, 15×. D. *D. divaricata* var. *viscidula* (holotype); petal, 7½×; sepal, 7½×; seed, 15×. E. *D. divaricata* var. *divergens* (holotype); petal, 7½×; sepal, 7½×; seed, 20×; habit, ½×.

43a. Drymaria divaricata var. divaricata ?

Drymaria divaricata HBK. Nov. Gen. & Sp. 6:24. 1832. (holotype: *Humb. & Bonpl. s. n.* Crescit ad litora Oceani Pacifici, prope Lima Peruvianorum, P *n. v.*)

Laxly spreading annuals, the internodes much longer than the leaves, to as much as 10 cm. long, minutely glandular-puberulent. Leaves opposite, the blades glabrous or minutely puberulent or villosulous, narrowly to broadly deltoid-ovate, 6–12 mm. long, 6–15 mm. broad, apically acute, marginally entire, basally truncate; the distally alate petioles 2–5 mm. long, the stipules filiform, caducous, mostly entire, 1.0–1.5 mm. long. Inflorescence of very lax terminal cymes, the flowers many, squarely campanulate; the glandular-puberulent peduncles to 10 cm. long; bracts oblong to lance-linear, ca. 1 mm. long; the pedicels glandular-puberulent, to as much as 35 mm. long. Sepals 5, glandular-puberulent to glabrous, unctuous, triangular-ovate, apically obtuse to acutish, and often cucullate, basally saccate, 3.0–4.5 mm. long; petals 5, 5–9 mm. long, bifid about two-thirds their length, the lobes narrowly spatulate, weakly 2–5-veined, apically obtuse, basally merging gradually with the linear claw, exauriculate to minutely denticulate; stamens 5, 3.5–5.0 mm. long, the anthers oblong 0.3–0.6 mm. long. Ovary at anthesis ovoid, the style trifid one-fourth to one-half its length 1.5–2.5 mm. long. Capsule ovoid, 2.5–3.5 mm. long, ca. 8-seeded, the seeds tightly circinnate, 0.8–1.5 mm. broad, coarsely tuberculate, the dorsal tubercles longer than broad, subdendritic. Fig. 15B (*Pennell 14560*).

Province of Lima, Peru.

Since I have not seen the type of *D. divaricata*, I sent specimens of all the varieties herein recognized to Dra. Lourteig for comparison with the Humboldt and Bonpland specimen in the Historical Herbarium at Paris. After comparison with the various specimens sent, she selected *Ferreyra 3460* as the best match for *D. divaricata* HBK. Also representing the typical variety is *Pennell 14560* which is illustrated in Fig. 15B. This has quite long petals proportionately much longer than those of *Ferreyra 3460*. Both specimens have peculiar dwarf flowers in the axils of some of the unusually small bracts. Both were collected at altitudes higher than 2700 meters, which might seem incompatible with the type locality, the description of which would at least suggest that *D. divaricata* might be a loma plant.

43b. Drymaria divaricata var. **stricta** (Rusby) J. Duke comb. & stat. nov.

Drymaria stricta Rusby in Phytologia 1:55. 1934. (holotype: *G. H. H. Tate 160.* Pongo de Quime Bolivia, alt. 12,000 ft. NY!)

Drymaria agapatensis Baehni & Macbride, in Field Mus. Bot. 13:619. 1937. (holotype: *Lechler 1947*; *Puno*, Agapata, G!; isotype at UPS, F, MO, P, etc.)

Upright or ascending lignescent annuals or perennials to as much as 30 cm. high, the internodes mostly longer than the leaves, minutely but obviously glandular-puberulent. Leaves opposite, glandular-puberulent, the blades ovate to reniform, apically acute, marginally entire or undulate, basally truncate to cordate, 5–14 mm. long, 5–20 mm. broad, the petioles often alate, 2–6 mm. long, stipules lacerate, the laciniae filiform to acicular, 1.5–2.0 mm. long. Inflorescence of

mostly terminal lax, several-flowered cymes, the peduncles 1–6 cm. long, glandular-puberulent, bracts oblong to lance-deltoid, 1–2 mm. long, mostly exceeded by the pedicels, these 1–10 mm. long, sepals 5, glandular-puberulent, ovate, basally saccate but not carinate, apically acute to shortly acuminate, subcucullate, 4.5–5.5 mm. long, weakly 3–4-nerved; petals 5, 4.5–5.5 mm. long, bifid for 2–3 mm., the lobes linear, obtuse to emarginate, narrowed to the linear claw, 1-nerved, usually auriculate; stamens 5, the anthers often aberrant, oblong to orbicular, ca. 0.3 mm. long; ovary at anthesis ovoid, the style about as long, 1.5–2.5 mm. long, trifid about half its length. Capsule 2.5–3.5 mm. long 2–8-seeded, the seeds tightly circinnate, 0.8–1.0 mm. broad, densely tuberculate, the dorsal tubercles secondarily tubercululate, the facial irregularly polygonal. Fig. 15C (Isotype of *D. agapatensis*).

Peru and Bolivia.

The seeds of this variety are among the most bizarre in *Drymaria*. Some specimens are referred here only reluctantly as they approach *D. glaberrima*, a species which shares the unusual tuberculation of the seeds.

43c. DRYMARIA DIVARICATA var. **viscidula** (A. Gray) J. Duke comb. & stat. nov.

Drymaria viscidula A. Gray, Bot. U. S. Expl. Exped. 1:124. 1854. (HOLOTYPE: *Wilkes exped. s. n.*; Obrajillo, Peru US!)

Upright annuals to as much as 35 cm., the internodes mostly longer than the leaves. Leaves opposite, the blades glabrescent, broadly ovate, apically acute and mucronulate, basally subcordate, 5–8 mm. long, 6–10 mm. broad, the veins very obscure; petioles 1–2 mm. long, glabrescent; stipules entire or bifid, the divisions linear, deciduous, 1.0–1.5 mm. long. Inflorescences of 3–9-flowered cymes, the peduncles rather densely glandular-pubescent; bracts linear, 1.0–2.5 mm. long, gradually reduced; pedicels 1.0–2.5 mm. long. Sepals 5, subequal, the outer glandular, broadly lanceolate, acute, strongly 3-nerved, 3–4 mm. long, ca. 1 mm. broad, the inner flatter, obtuse, 1.0–1.5 mm. broad, with scariose margins outside the 3 ribs; petals 5, 3.5–4.0 mm. long, bifid about half their length, the lobes oblong, ca. 0.5 mm. broad, basally auriculate, the auricles obtusely deltoid, the claw gradually tapering to the auricle; stamens 5, ca. 3.2 mm. long, the anthers oblong, ca. 0.5 mm. long; ovary at anthesis subglobose, exceeded by the anthers, the style trifid more than half its length, slightly exceeding the anthers. Capsule ovoid, 2.8–3.5 mm. long, maturing ca. 6 seeds, the seeds cochleate, ca. 0.7 mm. broad, dorsally tuberculate with low rounded tubercles broader than long, facially flattened or sulcate, merely lineolate. Fig. 15D (Holotype).

Peru, at rather high elevations.

Although in some respects (especially the seeds) suggestive of *D. glandulosa*, I think a perusal of the plate depicting the Series DIVARICATAE will convince one that the var. *viscidula* is more properly aligned here.

43d. DRYMARIA DIVARICATA var. **divergens** J. Duke var. nov.

Herbae annuae graciles diffusae glanduloso-pilosulosae internodis saepe quam foliis longioribus. Folia opposita laminis reniformibus apice rotundatis vel obtusis

mucronatisque basi truncatis aut rotundatis, 5–12 mm. longis, ea in ramis lateralibus saepe reducta petioli saepe in longitudine laminae foliorum aequales stipulis lanceolatis frequenter quam petiolis brevioribus. Flores in cymas terminales pleures dispositi pedicellis saepe divergentibus frequenter 2–4 × in longitudine pluribus quam floribus bracteis lanceolato-linearibus usque ad 3 mm. longis. Sepala 5, 3.5–4.5 mm. longa ovata acuta 3-nervata vix stipitato-glandulosa; petala 5, sepalis aequalia ut vix plus, bifida lobis angusto-spatulatis obtusis vel truncatis 3–5-nervatis basi auriculatis ungue lineari; stamina 5 quam petala brevioria, antheris oblongis ca. 0.6 mm. latis. Capsulae inclusae seminis cochleatis. Ca. 0.8 mm. latis tuberculatis tuberculis dorsalibus latis quam longioribus. Fig. 15E (Holotype).

Peru: Dept. Lima, prov. Pativilca; Lomas de Pacar, alt. 150–700 m. *O. V. Nuñez 2320* (holotype, US).

If I have erred in my interpretation of the typification of *D. divaricata* HBK, this variety of the Peruvian lomas would be my second choice, and indeed were it not for the kind assistance of Dra. Lourteig, I believe this new variety would be masquerading under the name *D. divaricata* HBK. The similarities of the two concepts are strong, but the slight morphological differences plus the ecologic separation seem to warrant varietal segregation.

43e. Drymaria divaricata var. **reflexiflora** J. Duke var. nov.

Drymaria divaricata Auct. Am. non HBK.

Plantae parvae ascendentes ad 25 cm. altae internodis quam foliis saepe longioribus glabris. Folia opposita glabris, eis in rostellam aggregatis spatulatis longe petiolatisque gradatim foliis caulis anguste ad late ovatis vel elliptico-ovatis acutis basi truncatis saepe undulatis (in marginibus) mixtis, eisdem etiam secundum breves alatos petiolos attenuatis, petiolis saepe quam stipulis brevioribus stipulis saepe trifidis lobis filiformibus, 1.0–2.5 mm. longis. Flores campanulata in laxas evidenter trichotomas cymas foliis veris ovatis bracteis conmixtis; bractea 2–4 mm. longae, acutae vel acuminatae, prope aequales vel praestantes divaricatis glabris pedicellis. Sepala 5, glabra ovata vel elliptica, 3.0–4.5 (–5) mm. longa evidenter 3-costata basim umbonata vix saccata exteriora acuta, interiora obtusa vel acuta; petala 5, vix exserta 3.0–4.5 mm. longa, 2/3-bifida lobis angusto-spatulata apice obtusa 3–7-nervata, basi auriculata vel biauriculata tum in unguem linearem constricta; stamina 5 antheris fertilibus saepe reductione 3 oblongis filamentis 3.0–3.5 mm. longis; ovarium ovoideum, 2.5–3.5 mm. longum, stylo 1.0–1.8 mm. longo, 1/2-fido trilobato. Capsule ovoideae, 15–25-seminiferes seminibus constricte circinatis ca. 0.6 mm. latis tuberculis dorsalibus latis quam longioribus scabris superficie tuberculis conicis vel ellipsoideis munitis. Fig. 15A (Holotype).

Peru: Dept. Lima, Prov. Chancay; Lomas de Chancay, 500–600 m.; *Ferreyra 11522.* (holotype, MO).

Although long confused with typical *D. divaricata* HBK., also reputed to be a loma plant, there is little doubt that this variety is distinct, morphologically and possibly ecologically. Plants representing this new variety bear little resemblance to var. *divaricata*, as depicted in a photograph of the type.

Q. Series CORDATAE

Leaves opposite, ovate to reniform, sessile to petiolate, entire, stipulate, the stipules entire or lacerate. Flowers in terminal cymes, rarely solitary in the axils. Sepals mostly acute, 1–3-nerved. Petals bifid (occasionally ligular in *D. xerophylla*), unguiculate, exauriculate (poorly defined auricles occasionally present in *D. gracilis*), the lobes 1-nerved (except *D. galeottiana*). Stamens 2–5, the anthers orbicular to oblong. Styles 2–3, free or basally united. Seeds 1–many, cochleate, tuberculate, the tubercles domical or rectanguloid, contiguous to remote. Five species, 1 more or less pantropical, 1 ranging from western U. S. A. to Argentina, the others confined to Mexico and vicinity. Figs. 16, 17, 18.

a. Petals about equaling the sepals, the lobes 1–4-nerved; sepals 1-nerved and carinate or 3-nerved and subcarinate; seeds numerous, less than 1 mm. broad:
  b. Leaves deltoid, long-petiolate, the stipules lacerate or entire, shorter than the petioles; petals divided more than half their length, the lobes 1-nerved:
    c. Stipules lacerate; seeds coarsely tuberculate, the tubercles approximate; continental Mexico and northern Central America.....44a. D. GRACILIS ssp. GRACILIS
    c. Stipules entire; seeds merely verruculose with remote protuberances. Baja California. .....44b. D. GRACILIS ssp. CARINATA
  b. Leaves ovate to reniform, subsessile, the stipules lacerate, longer than the petioles; petals divided about half their length, the lobes 2–4-nerved.....45b. D. GLANDULOSA var. GALEOTTIANA
a. Petals shorter than the sepals, the lobes 1-nerved; sepals trinerved; ecarinate (except *D. cordata* ssp. *diandra*); seeds 1–many, 0.5–2.0 mm. broad.
  d. Petals much shorter than the sepals, bilobed or ligular; seeds 0.5–0.8 mm. broad, the facial tubercles rectanguloid or lineolate, remote; stipules lacerate:
    e. Flowers in terminal cymes; leaves obviously petiolate; petals bifid; stamens 3–5; seeds 5–many; plants usually densely glandular.....45a. D. GLANDULOSA var. GLANDULOSA
    e. Flowers clustered in the axils of subsessile leaves; petals bifid or ligular; stamens 3, seeds 1–3; plants usually glabrous.....46 D. XEROPHYLLA
  d. Petals little to much shorter than the sepals, bilobed; seeds 0.7–2.0 mm. broad, the tubercles more or less domical and subcontiguous; stipules entire or lacerate:
    f. Leaves deltoid-ovate, the stipules entire; secondary veins forming a crinkled interrupted reticulum; stamens 4–5, seeds 3–5; styles united for half their length or more; southern Mexico, Guatemala and Bolivia.....47. D. LADEWII
    f. Leaves deltoid-ovate to reniform, the stipules lacerate; secondary veins obscure; stamens 2–5; seeds 1–12; styles completely free or united to half their length; pantropical complex:
      g. Flowers campanulate, the pedicels usually with a conspicuous glandular girdle; sepals ecarinate or subecarinate, glabrous to densely glandular, not apically incurved; stamens 2–5; seeds 1–12, 0.8–1.5 mm. broad; pantropical.....48a. D. CORDATA ssp. CORDATA
      g. Flowers pyriform, the pedicels without a clearly delineated girdle; sepals carinate, densely glandular, apically incurved; stamens 2 (–4); seeds 1–2 (–4), 1.5–2.0 mm. broad; Old World Tropics.....48b. D. CORDATA ssp. DIANDRA

44a. DRYMARIA GRACILIS ssp. GRACILIS

Drymaria gracilis Cham. & Schlecht. in Linnaea 5:232. 1830. (HOLOTYPE: *Schiede & Deppe 503*; prope Jalapa. B, *n. v.* isotype at GOET!)

Drymaria cordata var. γ *gracilis* (Cham. & Schlecht.) Rohrb. in Mart. Fl. Bras. 14^2:260. 1872.

Erect or ascending perennials to as much as 45 cm. tall; the internodes mostly longer than the leaves, glabrous or minutely stipitate-glandular; leaves opposite, the blades glabrous, rarely villosulous or punctate, deltoid-ovate (narrower upwards), 5–15 mm. long, 3–15 mm. broad, apically acute to rounded and apiculate, marginally entire, basally truncate 3–5-nerved, the petioles 1–8 mm. long; the stipules

bifid or trifid, 1.0–2.5 mm. long, the divisions filiform. Inflorescences of lax terminal, many-flowered cymes, the peduncles 2–6 cm. long; bracts ovate, carinate, 0.5–1.5 mm. long; pedicels 3–6 mm. long, glabrous, divaricate. Sepals 5, ovate, glabrous, 2.0–2.7 mm. long, apically acute, 1-nerved, carinate; petals 5, 2.0–2.7 mm. long, bifid at least two-thirds their length, the lobes obtuse to emarginate, basally entire to auriculate, divaricate, tapered or truncate to the minute claw; stamens 5, rarely fewer, 1.8–2.2 mm. long, the anthers oblong, 0.4–0.5 mm. long, briefly connate into a shallow cup; ovary at anthesis globose, the styles elongate, bifid or trifid less than half their length, exceeding the ovary; capsule globose, equaling or exceeding the sepals, 1.8–2.5 mm. long, many-seeded, the seeds cochleate, 0.5–0.6 mm. broad, coarsely tuberculate, the dorsal tubercles domical, the facial tubercles polygonal, approximate. Fig. 16B.

Fig. 16: A. *D. glandulosa* var. *galeottiana* (holotype); petal, 10×; sepal, 10×; seed, 22½×. B. *D. gracilis* ssp. *gracilis*; petal, 10×; sepal, 10×; seed, 20×; habit, ½×. C. *D. gracilis* ssp. *carinata* (isotype); petal, 10×; sepal, 10×; seed, 20×. D. *D. glandulosa* (holotype of *D. leptoclados*); petal, 10×; sepal, 10×. E. *D. glandulosa* (holotype of *D. fendleri*); petal, 10×; sepal, 10×; seed, 25×.

Hidalgo to Vera Cruz, Mexico.

Specimens in the Lund Herbarium, and the herbaria at Leningrad and the Field Museum, although labeled as grown from seeds of *D. divaricata*, are clearly referable to *D. gracilis*. Somewhere a mixup in labels must have occurred. For that reason, I sent a specimen of this species to Dra. Lourteig for comparison with the type of *D. divaricata*. As mentioned in the discussion of *D. divaricata* previously, she cited the Peruvian *Ferreyra 3460*, very different from the Mexican *D. gracilis*, as comparable to *D. divaricata* HBK.

44b. DRYMARIA GRACILIS ssp. **carinata** (Brandegee) J. Duke comb. & stat. nov.

Drymaria carinata Brandegee, in Zoe 2:70. 1891. (HOLOTYPE: *Brandegee 34*; Sierra de la Laguna, Baja Calif. UC!)

Drymaria carinata var. *perennis* Wiggins, in Proc. Cal. Acad. Sci. 4^{25}:197. 1944. (HOLOTYPE: *Gentry 4415*; La Laguna, Sierra Laguna UC!)

Prostrate to ascending annuals or perennials to as much as 40 cm. high, the internodes mostly longer than the leaves, glabrous. Leaves opposite, the blades glabrous, narrowly to broadly deltoid-ovate, 5–20 mm. long, 2–15 mm. broad, apically rounded to acute, marginally entire, basally truncate, 3-nerved, petioles 1–10 mm. long, the stipules entire, 1–2 mm. long, filiform. Inflorescences of terminal lax 3–many-flowered cymes, the peduncles 2–6 cm. long; bracts ovate, carinate, 1.0–1.5 mm. long, the pedicels 2–12 mm. long, glabrous. Sepals 5, ovate, glabrous, 1.5–2.5 mm. long, apically acute to acuminate, 1-nerved and carinate; petals 5, 1.5–3.0 mm. long, bifid at least two-thirds their length, the lobes apically obtuse to emarginate, 1-nerved, divaricate, basally auriculate to entire, abruptly truncate or tapered to the claw; stamens 3–5, 1.5–2.0 mm. long, anthers oblong 0.3–0.4 mm. long, shallowly connate into a cup; ovary at anthesis globose, the style trifid one-half to five-sixths its length. Capsule globose, 1.5–2.0 mm. long, many-seeded, the seeds cochleate, 0.4–0.6 mm. long, minutely and remotely tuberculate. Fig. 16C (Isotype).

Baja California, Mexico.

This subspecies shares with the typical subspecies the tendency toward perenniality. Probably separated for some time, yet obviously closely related, these subspecies exhibit an interesting disjunction.

45a. DRYMARIA GLANDULOSA var. GLANDULOSA

Drymaria glandulosa Presl, Rel. Haenk. 2:9. 1831. (HOLOTYPE: *Haenke s. n.*; habitat in Mexico, Pr!)

Drymaria ramosissima Schlecht. in Linnaea 12:206. 1838. (HOLOTYPE: *Hegewisch s. n.*, prope urbem Mexico, GOET (?) *n. v.*)

Drymaria leptoclados Hemsl. Diag. Pl. Nov. 2. 1878. (HOLOTYPE: *Bernoulli 240*, Guatemala; Camino del Sapote; K!; isotype at NY)

Drymaria fendleri S. Wats. in Proc. Am. Acad. 17:328. 1882. (HOLOTYPE: *Fendler 60*, New Mexico, GH!)

Drymaria leptoclados var. *peruviana* J. Ball, in Journ. Proc. Linn. Soc. 22:32. 1885. (HOLOTYPE: *J. Ball s. n.*; Chicla, Peru, K?; isotype (?) at GH!)

Drymaria blasiana M. E. Jones, Contr. West. Bot. 15:125. 1929. (HOLOTYPE: *M. E. Jones 22845*; in open places, San Blas, Sinaloa; POM!)

Drymaria fendleri var. *perennis* M. E. Jones, Extr. Contr. West. Bot. 18:65. 1933. (HOLOTYPE: *M. E. Jones 27050*, Laguna Mtns., Baja Cal. POM!; isotypes at UC, etc.)

Drymaria glandulosa var. *fendleri* (S. Wats.) Fosberg, in Morton, in Contr. U. S. Nat. Herb. 29:96. 1945.
Drymaria glandulosa var. *perennis* (M. E. Jones) Fosberg, loc. cit. 29:96. 1945.

Sparingly to densely stipitate glandular upright or ascending annuals or perennials, the internodes mostly longer than the leaves, the taproot to 1 cm. thick. Leaves opposite, the blades sparingly to densely glandular-puberulent, ovate to reniform, 5–12 mm. long, 5–20 mm. broad, apically rounded and apiculate, basally cordate, marginally entire, the petioles 1–8 mm. long; stipules lacerate, the divisions lance-linear to filiform. Inflorescences of terminal and rarely axillary lax to dense 5–many-flowered cymes, the peduncles (0–) 2–8 cm. long (the peduncles often axillary and abbreviated in var. *fendleri*); bracts lanceolate-aristate 2.5–5.0 mm. long, often exceeding the pedicels (especially in var. *fendleri*), lanceolate, weakly to strongly 3-ribbed, the ribs subapically confluent, the mid-rib often excurrent, the outer sepals frequently conspicuously shorter than the inner and more attenuate at the apex, 3.0–4.6 mm. long; petals 3–5, 1.2–3.0 mm. long, bifid about half their length, the lobes linear, apically acute to emarginate, 1-nerved, basally auriculate or entire; stamens 2–5, the anthers oblong, 0.2–0.4 mm. long, the filaments 1–2 mm. long; ovary at anthesis subglobose, longer than the style, the style bifid or trifid about half its length; capsule 1.5–2.8 mm. long (2–) 4–20-seeded, the seeds cochleate, 0.5–0.8 mm. broad, minutely but regularly tuberculate, the dorsal tubercles domical, the facial tubercles rectanguloid or lineolate, remote. Fig. 16D (Holotype *D. leptoclados*); Fig. 16E (Holotype *D. fendleri*).

Baja California; Arizona through western South America along the Andes to Argentina; apparently skipping southern Central America.

Fosberg (in Contr. U. S. Nat. Herb. 29:96. 1945) recognizes three varieties of *D. glandulosa,* a variable species indeed. The varieties are separated on basis of varying vegetative characters, var. *fendleri* having subglabrous leaves and var. *perennis* being perennial. Var. *fendleri* also tends to have cinereous less cordate leaves and more dense inflorescences. Although the type of *D. glandulosa* was described as being an annual, the root is apparently perennial and nearly 3 mm. thick. Since the perennial habit occurs in both the subglabrous and the densely pubescent forms and all possible combinations of the characters can be found throughout the range of the species I see little reason for their recognition.

Some of the forms are only with difficulty separated from *D. cordata,* but the seeds of the two have markedly different sculpture. *Drymaria glandulosa* is also marked by longer anthers and proportionately longer inner sepals, and the inflorescence is more obviously cymose with a conspicuous central leader. The perennial habit, frequently encountered in *D. glandulosa,* is rarely if ever encountered in *D. cordata.*

Mandon 950 from the Andes of Bolivia (2600–2700 m.) dept. Larecaja, referred tentatively by Ball (Kew Bull. 22:32) to *D. leptocladus* var. *peruviana* is obviously *D. glandulosa,* and in its tendency toward glabrescence it does resemble *D. leptocladus.*

Berlandier 999 and *1122* from Mexico are distinctive in that the petals have pli-nerved veins and subcylindric tubercles thus suggesting intergression with a member of the Series VILLOSA.

45b. DRYMARIA GLANDULOSA var. **galeottiana** (Briq.) J. Duke comb. & stat. nov.

Drymaria galeottiana Briq. in Ann. Conserv. & Jard. Bot. Gen. 13:373. 1911. (HOLOTYPE: *Galeotti 4408*; near Oaxaca, Mexico, G!; isotypes at K [sub *4416*] and L.)

Rather delicate erect annuals to as much as 20 cm. high, the internodes mostly longer than the leaves, glandular-puberulent, the roots fusiform. Leaves opposite, the blades glandular-puberulent and glabrescent, broadly ovate to reniform, apically obtuse and apiculate, marginally entire, basally truncate to subcordate, subsessile, the stipules bifid or trifid, 1–2 mm. long, about equaling the petioles. Flowers obconic, in rather dense terminal cymes, the peduncles 1–2 cm. long, glandular-puberulent; bracts ovate, aristate to acuminate, 1.5–2.0 mm. long, about equaling all but the central pedicels which may be up to 6 mm. long. Sepals 5, subequal, glandular-puberulent, 3.0–3.6 mm. long, 1.5–2.8 mm. broad, ovate to broadly oblong, 3-nerved, the midrib sometimes prominent and excurrent, the inner sepals obtuse, the outer acute, transparent save for the nerves; petals 5, 2.5–3.2 mm. long, bifid ca. half their length, the lobes oblong, obtuse, 2–4-nerved, tapering gradually to the claw, exappendiculate; stamens 3–5, 1.5–2.2 mm. long, the anthers suborbicular, 0.2–0.3 mm. long; ovary at anthesis subglobose, the style ca. 1 mm. long, trifid ca. half its length. Mature capsule subglobose, 2.5–3.0 mm. long, many-seeded, the seeds cochleate, about as long as broad, ca. 0.6 mm. broad, the dorsal tubercles low and domical, the facial tubercles rectangular, somewhat remote. Fig. 16A (Holotype).

Known only from few scattered collections in Oaxaca and Hidalgo, Mexico.

At Kew, the specimen labeled 4416 is called *D. galeottiana* and that labeled 4408 is called *D. nummularia*, so apparently the labels have been crossed. This variety is a misfit in this series because of the petal nervation and it may prove to represent a mere hybrid. The seeds, sepals, and pubescence suggest *D. glandulosa* whereas the nervation of the petals and to some extent their shape and size, recall *D. laxiflora*. These two are the most likely candidates for the parents if indeed the plant is a hybrid.

46. DRYMARIA XEROPHYLLA A. Gray, Pl. Wright. 2:18. 1852. (HOLOTYPE: *Coulter 722*).

Ascending perennials profusely branched from the base, the internodes longer or shorter than the leaves, glabrous. Leaves opposite, the blades broadly to narrowly ovate, glabrous, strongly 3–7-nerved, 5–10 mm. long, 3–10 mm. broad, apically acute and apiculate, marginally entire, basally rounded to obtuse, subsessile; the stipules lacerate, the divisions lance-linear to filiform, exceeding the petioles. Inflorescences of dense axillary cymes, or fascicles, the lanceolate acuminate bracts longer than the glabrous peduncles and pedicels, 1.5–2.5 mm. long. Sepals 5, oblong, apically acute to obtuse, strongly 3-nerved with the nerves subapically confluent, basally umbonate, 3–4 mm. long, glabrous to scantily stipitate-glandular; petals 3–5, entire and ligulate or bifid for half their length, the lobes apically

Fig. 17: *D. xerophylla*; sepal, 15×; petal, 15×; seed, 15×; habit, ½×.

denticulate or entire, 1-nerved, 1.0–1.8 mm. long; stamens 3, ca. 1 mm. long, the anthers oblong, the filaments basally connate into a shallow cup; ovary at anthesis subglobose, the style about as long, bifid or trifid about half its length. Capsule ellipsoid, 3-valved, 1–3-seeded, the seeds cochleate, 0.7–0.8 mm. broad, minutely tuberculate or merely reticulate on the facies. Fig. 17.

San Luis Potosí to Oaxaca, Mexico.

47. Drymaria ladewii Rusby, in Phytologia 1:54. 1934. (holotype: *G. H. H. Tate 652*: Bolivia; Nequejahuira; alt. 8000 ft. NY!)

Drymaria hypericifolia Auct. Am. non Briq.

Diffusely spreading annuals or perennials, the internodes much longer than the leaves, strongly divaricate, viscid-puberulent. Leaves opposite, the blades glabrous,

deltoid-ovate, apically rounded to acute and apiculate, marginally entire, basally more or less truncate; stipules entire, more or less lanceolate; larger leaves to 2.8 cm. long, 2.5 cm. broad, trinerved, with the secondary veins forming an obvious but interrupted reticulum, the leaves as the rather long petioles strongly reduced upwardly. Inflorescences of terminal and axillary 5–many-flowered cymes, the axes glandular-puberulent, the bracts lanceolate, 1.5–3.0 mm. long, exceeded by the long, divaricate pedicels, the pedicels to 12 mm. long. Sepals 5, lance-oblong, 2–3 mm. long, apically obtuse or acute by extension of the midrib, weakly 1–3 nerved, the midrib often distally subcyanic; petals 5, about equaling the sepals in length, bifid about three-fourths their length, the lobes obtuse, exauriculate, subdivaricate, weakly 2–5-nerved, the claw carnose, subcylindric; stamens 5; 1.5–2.5 mm. long, the oblong anthers ca. 0.5 mm. long, the filaments basally connate into a more or less carnose ring; ovary at anthesis turbinate, the style trifid ca. half its length, about attaining the anthers. Capsule turbinate, 3-valved, included (seeds rarely mature in the specimens at hand), 1–5-seeded, the seeds similar to those of *D. cordata*. Fig. 18A.

Southern Mexico, Guatemala, Bolivia.

After scrutiny of the copious Guatemalan material and the scanty Bolivian material (2 specimens, one from the O. Kuntze herbarium, the other the type; [the second specimen cited by Rusby, in his description of the species, apparently is a hybrid with *D. cordata* or some related species and must be excluded from *D. ladewii*]), I am unable to find the slightest differences between them. Asserting rather strongly that there is no obvious difference between the Guatemalan and Bolivian material, I am quite at a loss to explain the peculiar disjunction exhibited by this species.

48a. DRYMARIA CORDATA (L.) Willd. ex Roem. & Schult. Syst. Veg. 5:406. 1819. (LECTOTYPE after Mizushima: Linnaean Herbarium specimen no. 109-1; LINN *n. v.*)

Holosteum cordatum L. Sp. Pl. 88. 1753.
Holosteum diandrum Sw. Prodr. 27. 1788. (HOLOTYPE: habitat in Jamaica, S!)
Drymaria diandra MacFadyen, Fl. Jam. 1:52. 1837. not Blume, 1825.
Drymaria cordata β *diandra* (Sw.) Griseb. Fl. Brit. W. Ind. 56. 1859.
Drymaria cordata β *puberula* Tr. & Pl. in Ann. Sci. Nat. 4^{17}:148. 1862. (HOLOTYPE: *Triana s. n.*; Bogota alt. 2600 m., P, *n. v.*; isotype at NY!)
Drymaria procumbens J. N. Rose, in Contr. U. S. Nat. Herb. 1:304. 1895. (HOLOTYPE: *Palmer 1165*, near water about Colima, Mex., US!; isotype at GH)
Drymaria adenophora Urban, in Fedde, Repert. Sp. Nov. 21:213. 1925. (HOLOTYPE: *Ekman 12978*, Cuba; prov. Pinar del Río prope Cortez, B?; isotype at G, S, NY!)
Stellaria adenophora (Urb.) León in León & Alain, Flora de Cuba 2:154. 1950.
Drymaria cordata var. *pacifica* Mizushima, in Jour. Jap. Bot. 32:78. 1957. (HOLOTYPE: *Svenson 65*; Academy Bay, Indefatigable Island, Galapagos Islands, 100 ft. alt.; GH!)

Glandular-puberulent to glabrate ramifying annuals, prostrate and spreading or erect, the internodes mostly longer than the leaves, glabrous to densely glandular, often rooting at the nodes. Leaves glabrous to scantily puberulent, orbicular to reniform, apically rounded and occasionally mucronulate, basally rounded to cordate, 5–25 mm. long, 5–30 mm. broad, the petioles 2–15 mm. long; stipules mostly lacerate, rather persistent, to 2 mm. long. Inflorescences of terminal or

axillary few–many-flowered dichasial cymes, (flowers rarely solitary in the axils) the bracteate pedicels locally girdled with a dense band of glandular pubescence, rarely subglabrous, 2–15 mm. long, much exceeding the subtending bracts. Sepals 5, lanceolate to ovate, acute, glandular-puberulent to glabrous, obscurely to strongly 3-nerved, 2.5–4.0 (–5.0) mm. long, the borders translucent; petals 5, 2–3 mm. long, deeply bifid, the lobes linear, acute, rarely obtuse, 1-nerved, basally exauriculate but rarely subdentate; stamens 2–3 (–5), the flattened filaments 2.0–2.5 mm. long, the anthers suborbicular, 0.2–0.3 mm. long; style 0.5–1.0 mm. long, bifid or

Fig. 18: A. *D. ladewii*; sepal, 10×; petal, 10×; androecium, ca. 10×; seed, 15×; habit, ½×. B. *D. cordata* ssp. *cordata* (holotype of var. *pacifica*); petal, 10×; sepal, 10×; seed, 15×. C. *D. cordata* ssp. *cordata* (holotype of *D. procumbens*); aberrant petal, 7½×; normal petal, 7½×; sepal, 7½×; seed, 15×. D. *D. cordata* ssp. *diandra* (type of *D. retusa* ?); petal, 12½×; sepal, 12½×. E. *D. cordata* ssp. *diandra* (lectotype); petal, 10×; sepals, 10×.

trifid from half to its entire length; ovules few to many, campylotropous on free central placentae. Capsule ovoid, 1.5–2.5 mm. long, the 3 valves entire; seeds 1–many, 1.0–1.5 mm. broad, cochleate, dark reddish brown, tuberculate in lines, all the tubercles low and domical, closely approximated or contiguous. Fig. 18B (Holotype of var. *pacifica*); Fig. 18C (Holotype of *D. procumbens*).

A nearly pantropical species, in America ranging from Florida and Mexico through the West Indies and Central America to Argentina.

Mizushima (in Jour. Jap. Bot. 32:69. 1957), studying the varietal potentials of this polymorphic species, described var. *pacifica*, which differs from typical *cordata* in having glabrous sepals, more seeds, and a tendency to have a greater number of stamens and the styles divided completely to the ovary. This rather striking variety seems to be lacking in continental North America. Occuring in both var. *pacifica* and var. *puberula*, for those who wish to recognize them, are variants in which the flowers are subsolitary in the axils (e.g. *Holton 733* from Colombia). Surprisingly and fittingly these have as yet received no taxonomic status. *Drymaria adenophora* Urban represents a more or less viscid form with diminutive leaves and flowers and apparently is very similar to specimen 109-1 in the Linnaean herbarium. A similar reduction is exhibited by the type of *Holosteum diandrum* Sw. generously loaned by Stockholm. *Mosen 405* at Lund from Brazil with the sepals to as much as 5.2 mm. long represents the opposite extreme of *D. adenophora*, which I believe is typical *D. cordata*.

Perhaps the strangest aberration is that represented by the flowers of the type of *D. procumbens*, here considered to represent only a monstrosity. The petals are bilobed but one of the lobes is clearly staminal in nature (see Fig. 18C), the other lobe being normal and petaloid. I have seen a similar aberration in one specimen of *D. paposana* var. *weberbaueri*, perhaps lending weight to Pax's interpretation of the petals as staminodia.

48b. DRYMARIA CORDATA ssp. **diandra** (Blume) J. Duke comb. & stat. nov.

Drymaria diandra Blume, Bidjr. Fl. Nederl. Ind. 62. 1825. (LECTOTYPE: after Mizushima, sect. 99, 143–199 at L!)
Drymaria retusa Wallich, ex Wight & Arnott, Prodr. Fl. Ind. Or. 359. 1834. as synonym. (? TYPE?: *Wight 152*, G, L, !)
Drymaria cordata forma *indica* Miquel, in Junghuhn, Pl. Jungh. 395. 1855.
Drymaria extensa Wallich, ex Edgeworth, & Hook. f. in Hook. f. Fl. Brit. Ind. 1^2:244. 1874. (? TYPE?: *Wallich 647*, G!)
Drymaria gerontogea F. Muller, Descr. Papuan Pl. 1:87. 1877.

Prostrate or ascending annuals, the internodes longer than the leaves, glabrous to stipitate-glandular. Leaves opposite, the blades glabrous, rarely minutely puberulent, deltoid-ovate to orbicular or subreniform, apically rounded and often apiculate, marginally entire, basally truncate to obtuse, rarely cordate, 5–25 mm. long, 3–20 mm. broad, 3–7-nerved; the petioles 2–8 mm. long usually exceeding the stipules; the stipules lacerate, the segments filiform, 1–3 mm. long. Inflorescence a terminal lax to dense 3–many-flowered cyme, the peduncles 1–12 cm. long, glabrous or glandular-puberulent; bracts lanceolate, 2–5 mm. long; pedicels evenly glandular-puberulent; 1–8 mm. long. Sepals 5, narrowly obovate, 2.0–4.5 mm. long, the outer glandular-puberulent, strongly carinate, strongly three-ribbed, the

ribs protrusive and often connected by cross-veins; petals 3–5, 1.5–3.0 mm. long, bifid one-half to two-thirds their length, the lobes oblong, 1-nerved, apically obtuse to emarginate, basally tapered to the linear claw. Stamens 2–3 (–4), 1.6–2.2 mm. long, the anthers suborbicular, the filaments basally connate into a shallow cup (the cup often carnose in African forms). Ovary at anthesis globose, the styles short, bifid or trifid from half to all their length. Capsule 2–3-valved, 1.5–2.5 mm. long, 1–2-seeded, the seeds cochleate, 1.4–2.0 mm. broad, rather densely tuberculate. Fig. 18D (type of *D. retusa* ?); Fig. 18E (lectotype of *D. diandra*).

Tropical Africa, Australia, and Tropical Asia (China, S. & W.; India, Indochina, Malaysia, Formosa, Ryukyu Archipelago), Oceania, Hawaii, Philippines, New Guinea, Celebes.

Mizushima (in Journ. Jap. Bot. 32:69. 1957), after a detailed study of the variation of *D. cordata*, reinstated *D. diandra*, long lost in synonymy under *D. cordata*, to specific status. Intermediates do occur between the two, especially in Africa. The absence of the taxon from the New World when weighed with the characters enumerated in the key, none of them invariably constant, suggest that reduction to a subspecies more truly reflects the hierarchial relationships.

African forms are very perplexing and differ from the typical material in the large sepals and petals, higher number of stamens, with prominent, often carnose, staminodial cups. The flowers often lack the pyriform shape which so frequently differentiates ssp. *diandra* from ssp. *cordata*. Description of these variants as formal taxa would seem to serve no purpose.

Species Excludendae

D. filiformis Benth. = *Stellaria filiformis* (Benth.) Mattf.
D. idiópoda S. F. Blake = *Stellaria* sp.
D. mairei Leville = *Cerastium* sp.
D. palmeri Hemsl. = *Stellaria* sp.
D. rotundifolia Harriot = *Stellaria rotundifolia* Poir. fide Kew Index

Species non Satis. Notae

D. adiantoides Muschl. (type: *Sodiro 1291*) ex char. = *D. villosa*?
D. grandiflora Schlecht. non Bartl. May be *Stellaria*?
D. megalantha Steud. " "
D. oxalidea Pax (type: *Schaffner 827*) ex char. veg. = *D. excisa*???
D. peruviana Muschl. (type: *Weberbauer 2601*) ex char. veg. = *D. divaricata*?
D. sessiliflora Fiori (Descr. non viso) ex geogr. = *D. cordata*

Combinationes et Taxa Novae

D. holosteoides var. *crassifolia* (Benth.) J. Duke
D. arenarioides ssp. *peninsularis* (S. F. Blake) J. Duke
D. barkleyi J. Duke & Steyermark
D. conzatti J. Duke
D. effusa var. *confusa* (J. N. Rose) J. Duke

D. effusa var. *depressa* (E. L. Greene) J. Duke
D. leptophylla var. *cognata* (S. F. Blake) J. Duke
D. leptophylla var. *nodosa* (Engelm.) J. Duke
D. engleriana var. *devia* (Baehni & MacBride) J. Duke
D. villosa ssp. *palustris* (Cham. & Schlecht.) J. Duke
D. villosa ssp. *palustris* forma *townsendii* (Robins.) J. Duke
D. villosa ssp. *palustris* var. *perennis* J. Duke
D. villosa ssp. *villosa* forma *tepicana* (M. E. Jones) J. Duke
D. villosa ssp. *paramorum* (S. F. Blake) J. Duke
D. paposana var. *serrulata* J. Duke
D. paposana var. *weberbaueri* (Muschl.) J. Duke
D. rotundifolia var. *nitida* (J. Ball) J. Duke
D. divaricata var. *stricta* (Rusby) J. Duke
D. divaricata var. *viscidula* (A. Gray) J. Duke
D. divaricata var. *divergens* J. Duke
D. divaricata var. *reflexiflora* J. Duke
D. gracilis ssp. *carinata* (Brandegee) J. Duke
D. glandulosa var. *galeottiana* (Briq.) J. Duke
D. cordata ssp. diandra (Blume) J. Duke

Citation of Specimens

U. S. A.

D. CORDATA (L.) Willd.
Fredholm 6487
Godfrey, R. K. 58025
McFarlin, J. B. 3192
Reese, W. D. 1506
Schallert, P. O. 7500
Small, J. K. 12761
Small, Britton & DeWinkeler 9310
Small, Mosier & DeWinkeler 10836
Steyermark, J. 63326

D. EFFUSA var. EFFUSA
Blumer 1639; 3368 (appr. *leptophylla*)
Harrison & Kearney 8088
Lemmon 509; 2644
Rothrock 169; 619
Wright 869 (TYPE)

D. EFFUSA var. DEPRESSA (Greene) J. Duke
Gould & Robinson 4961
Metcalfe 1428 (aber.); 1430 (TYPE)
Neally 251

D. GLANDULOSA Presl
Arséne 19280; 21665
Barkley 14NM715
Earle & Earle 460
Eggleston 16381; 16469a
Fendler 60 (TYPE: *D. fendleri*)
Gould & Haskell 4050
Green 12599
Hanson & Hanson A962
Harrison & Kearney 6104
Hinckley 500
Jones, M. E. 96; 28677
Metcalfe 793, 1378
Mulford 1187
Purpus 8147
Rose & Fitch 17647
Rusby 42
Shreve 7768
Standley 14047
Wooton 641
Wright 866

D. LAXIFLORA Benth.
Cory 30590
Hinckley 321, 357, 2847
Innes & Moon 1136
Moore & Steyermark 3044
Warnock W812

D. LEPTOPHYLLA (Cham. & Schlecht) Fenzl ex Rohrb.
Arséne 19375
Blumer 1411
Cory 30375
Darrow 3517
Darrow et al. 1485

Fendler 56
Greene 332; 12778
Harrison & Kearney 6187
Hinckley 1290
Metcalfe 527 (appr. *effusa*)
Purpus 8150
Rusby 41
Standley 13932
Wright, C. 868

D. MOLLUGINEA (Lag.) Didr.

Arséne 18596; 19073
Blumer 1433; 2100; 3583
Eggleston 10943; 15989
Ellis 405
Fendler 55 (TYPE: *D. sperguloides*)
Fulton 7368
Gould 3962
Gould & Haskell 4049
Greene 12600
Hanson & Hanson 952
Harrison, Kearney & Hastings 6228; 8092
Kearney & Peebles 10042; 12723
Lemmon 3002
Metcalfe 349; 1424
Mulford 806
Parker & McClintock 7509
Purpus 8148
Rusby 40
Standley 14212
Wooton 593
Wright 867

D. PACHYPHYLLA Woot. & Standl.

Cory 30793
Eggleston 19345; 19353
Havard 118
Hershey 3012
Hinckley 3522
Wooton 405 (TYPE)

MEXICO (Continental)

D. ANOMALA S. Watson

Bell & Duke 16581
Johnston & Muller 622A
Palmer 358; 700
Pringle 2847 (TYPE); 3278
Stanford, Retherford & Northcraft 485

D. ARENARIOIDES Humb. & Bonpl. ex Roem. & Schult.

Bonpland 4070 (TYPE?)
Coulter 698
Kenoyer 1882, 2447
Kirkwood 210
LeSueur 467, 622
Lundell 5351
Moore, H. E. 1566
Muller, C. H. 3342
Parry & Palmer 49
Pringle 236, 518, 715, 3539; 7589; 7927
Purpus 133, 1123
Rose, Painter & Rose 8719
Schaffner 139, 541
Shreve 6673; 7322; 9205
Thurber 815
White, S. S. 2477
Wiggins 7235

D. AXILLARIS Brandegee

Purpus 4526 (TYPE)

D. BARKLEYI J. Duke & Steyermark

Hernandez, Rowell & Barkley 16M531
Warnock & Barkley 14826M (TYPE)

D. CONZATTII J. Duke

Conzatti 1688 (TYPE)

D. CORDATA (L.) Willd.

Berlandier 1217
Ervendberg 228
Hinton 7442 (var. *pacifica*)
Karwinsky 29
Kerber 70, 180
Martinez-Calderon 408
Matuda 2287
Mexía 1309
Palmer 1165 (TYPE: *D. procumbens*)
Pringle 11805
Rovirosa 328
Seaton 477

D. EFFUSA var. EFFUSA

Thurber 995

D. EFFUSA var. DEPRESSA (Greene) J. Duke

Barkley, Rowell & Westlund 77
Nelson 4892
Orcutt, 3729, 3724
Ortenburger, Paxton & Barkley 16M699
Pringle 6480
Reiche 811
Rose 2156 (appr. var. *confusa*)
Rose & Hay 6243
Rose & Painter 7037; 7206; 7914

D. EFFUSA var. CONFUSA (Rose) J. Duke

Knobloch 1298
Maysilles 7773-A, 7441
Nelson 4813
Palmer 59 (TYPE)

D. ELATA I. M. Johnston

Johnston 7823 (TYPE)

Purpus 4496
Stewart 2651

D. EXCISA Standl.

Arséne 8450
Hinton 508; 4919; 5074; 5427 (TYPE: *D. grandis*); 5429; 9007
McVaugh 10153; 10247; 13421
Mexía 1748 (TYPE)

D. GLANDULOSA Presl

Aguilar 1782
Arséne 513; 595; 2295 (appr. *laxiflora*)
Bartlett 10312
Berlandier 677; 841; 1122; 1308
Bourgeau 283; 552; 592a
Chase 7216; 7354
Drouet & Richards 3907
Edwards 804B
Gentry 1338
Jones, M. E. 22845, 27050 (TYPE: *D. fendleri* var. *perennis*) 27051
Kenoyer 1153
MacDaniels 752
McVaugh 16790
Moore 1471; 3064
Orcutt 4332; 4337
Palmer 760
Parry & Palmer 51
Pringle 5089; 7122
Purpus 430; 3311
Rose & Hay 5511
Rose & Painter 6617; 6775; 7083 (appr. var. *galeottiana*) 7735
Rose, Standley & Russell 12697
Rowell, Webster & Barkley 17M470
Schaffner 130
Schaumann 332b
Seaton 476
Sessé, Mociño et al. 446, 447, 1394?

D. GLANDULOSA var. GALEOTTIANA (Briq.) J. Duke

Galeotti 4408 (TYPE); 4418

D. GRACILIS Cham. & Schlecht.

Barnes & Land 665
Botteri 349
Botteri & Sumichrast 1567
Bourgeau 2659
Fischer 642, 643
Loesener 138
Matuda 0905
Moore 2965
Müller 720, 775; 879
Rose & Hay 6114
Rose & Hough 4939
Smith, J. G. 360

D. HYPERICIFOLIA Briq.

Jurgenson 38 (TYPE)

D. LADEWII Rusby

Matuda 2008; 2283; 2994; 4000

D. LAXIFLORA Benth.

Arséne 1905; 5129
Balls B4472
Bartlett 10434
Bell & Duke 16772
Bourgeau 21, 2946
Coulter 706 (appr. *gracilis*); 710
Dugés 1880
Fisher 44293
Johnston 44293
LeSueur 1321
Lloyd 370
Lundell 5095
Marsh 871
Meyer & Rogers 2493; 2526
Moore 1489; 2033
Mueller & Mueller 1117
Orcutt 3910, 3915, 3929
Ortenburger, Paxton & Barkley 16M682; 16M693; 16M747
Palmer 253; 266
Parry & Palmer 57
Pringle 331 (TYPE: *D. chihuahuensis*) 4175; 6972
Purpus 3310
Rose 2789
Rose & Hay 5510, 5676, 5973
Rose & Painter 7148; 7207
Rose, Painter & Rose 8449; 8488; 8773; 8882
Rose, Standley & Russell 12796
Rusby 361
Schaffner 130 p. p.; 364; 366
Schumann 332a
Sessé, Mociño et al. 449; 468; 983
Shreve 9039; 9302
Stewart 2545
Stewart & Johnston 2124
Wynd & Mueller 620

D. LEPTOPHYLLA (Cham. & Schlecht) Fenzl. ex Rohrb.

Barlow 30
Coulter 697
Gentry 8474
McVaugh 13105
Palmer 497; 794
Parry & Palmer 60
Pringle 581; 1194; 6482
Purpus 3734
Rose 2690
Rose & Painter 7132
Schaffner 140; 388

D. LEPTOPHYLLA var. COGNATA (S. F. Blake) J. Duke

Maysilles 7545
Palmer 912 (TYPE)
Pennell 18819
Schaffner 542 p. p.

D. LEPTOPHYLLA var. NODOSA (Engelm.) J. Duke

Gentry 571M; 1814; 2669 (TYPE: *D. gentryi*)
Hartman 138
Knobloch 5522; 5615
LeSueur 258; 623 (sensu *gentryi*)
Muller 3426
Pringle 581; 716; 1195; 13506
Rose & Painter 6668
Schaffner 5
Townsend & Barber 201 (sensu *gentryi*)
Tucker 2457
White 2366; 2557; 2733; 4185; 4403; 4776 (aber.)

D. LONGEPEDUNCULATA S. Watson

Hinton 1957; 11284
McVaugh & Koelz 897
Pringle 2121 (TYPE) 3594; 4348

D. LYROPETALA I. M. Johnston

Johnston 7064; 7513; 7594 (TYPE): 8352; 9347
Johnston & Muller 241
Marsh 1571
Stewart 567 (TYPE: var. *coahuilana*)

D. MALACHIOIDES Briq.

Galeotti 4415 (TYPE)
Hinton 15505 (?)
Leavenworth 595 (?)

D. MOLLUGINEA (Lag.) Didr.

Arséne 1616
Griffiths 6749
Mearns 2248
Pringle 1192; 1571; 6481
Sessé, Mociño et al. 984
White 970

D. MULTIFLORA Brandegee

Arséne 5309; 6710
Gentry 6479
Hinton 1549; 2596; 6578; 11538; 12167; 12489; 15050; 15263
McVaugh 12962; 13441; 13442; 14066; 16524
McVaugh & Koelz 1264
Nelson 1787
Purpus 1653 (TYPE)
Rose & Painter 6517; 6773 p. p.; 6774; 7219
Schaffner 51; 367
Sessé, Mociño et al. 5005

D. PACHYPHYLLA Woot. & Standl.

Johnston 7684; 7790; 8009; 8925; 8335B
Johnston & Muller 787; 1108; 1234
Nelson 6375
Orcutt 1325
Pringle 5539
Purpus 472; 4942
Stewart 1161; 1745; 2956
Waterfall 13281

D. POLYCARPOIDES A. Gray

Gregg s. n. (TYPE)
Johnston 7344; 7841
Johnston & Muller 335; 761
Palmer 73
Purpus 4498
Stewart 814; 843; 1102; 1152; 1753

D. STIPITATA Fosberg

Muller 3301 (TYPE)
Rozynski 100; 486
Stewart 1093

D. SUBUMBELLATA I. M. Johnston

Johnston 8489 (TYPE)

D. SUFFRUTICOSA A. Gray ex S. Watson

Palmer 74 (TYPE)
Stewart 2813; 2916

D. TENUIS S. Watson

Arséne 2587; 6651
Berlandier 1177
Bourgeau 553
Kenoyer A-457
McVaugh 16795; 17768
Pringle 2120 (TYPE); 4096; 4536 (TYPE: var. *jaliscana*) 7648; 11928
Schaffner 363; 416
Seaton 267 (TYPE: *D. filiformis*)
Sessé, Mociño et al. 448, 466; 467; 5184

D. VILLOSA Cham. & Schlecht.

Arséne 5129 p. p.; 5214; p. p.; 5281; 6810
Bell & Duke 16648
Botteri 350; 944
Botteri & Sumichrast 568
Feddema 1095
Fischer 2092
Galeotti 1726; 4414
Hinton 1384; 5152; 9471
Jones, M. E. 22847 (TYPE: *D. tepicana*); 27051a (TYPE: *D. barrancae*)
Leavenworth & Hoogstraal 1295
Matuda 4752

Müller 120; 575a
Orcutt 4614
Palmer 748; 945; 1166; 1602
Pringle 1196; 1572
Purpus 4440, 6303; 10229
Rose 2078
Rose & Painter 6967; 7436
Rose, Standley & Russell 14145 & 14386 (both f. *tepicana*)
Schiede & Deppe 505 (TYPE)
Seaton 32
Sezaya, Paxon & Barkley 16M833
Sumichrast 1568; 1945

D. VILLOSA ssp. PALUSTRIS (Cham. & Schlecht.) J. Duke

Arséne 16; 5191; 5391; 5416; 5911
Balls B4568; B5504
Barkley et al. 7489
Frye & Frye 2606
Galeotti 4416 (TYPE: *D. nummularia*)
Hinton 3304; 11851; 12233
Jones, M. E. 90 (TYPE: *D. subsessilis*)
LeSueur 1322 (f. *townsendii*)
Leavenworth 525
Maysilles 7782
McVaugh 13415; 16159
Moore 2801; 2955
Palmer 616 & 711 (both f. *townsendii*)
Parry & Palmer 56
Pringle 1501; 7296
Rose & Hay 4800
Schiede & Deppe 405 (prob. transnumeration of TYPE number)
Townsend & Barber 231 (TYPE: *D. townsendii*)

D. VILLOSA ssp. PALUSTRIS var. PERENNIS J. Duke

Edwards 804B
Johnston 8965
Kenoyer 2449 (appr. *laxiflora*)
Moore 1669
Palmer 187 (TYPE); 356
Pringle 3265

D. XEROPHYLLA A. Gray

Arséne 46
Coulter 722 (TYPE)
McVaugh 16793
Parry & Palmer 50
Pringle 6910
Purpus 3309
Rose et al. 9679
Schaffner 525
Sessé, Mociño et al. 5003

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D. ARENARIOIDES ssp. PENINSULARIS (S. F. Blake) J. Duke

Carter et al. 2257
Craig 738
Dawson 1189
Howell 10576
Johnston 3972 (TYPE: *D. johnstonii*)
Purpus 337; 423 (TYPE); 496
Rose 16357
Xantus 5

D. DEBILIS Brandegee

Brandegee 35 (TYPE: *D. polystachya*); s. n. Feb. 13, 1889 UC (TYPE)
Carter 2578
Carter & Ferris 3709; 3812; 4093
Carter & Kellogg 2922
Collins, Kearney & Kempton 157; 211
Dawson 1095
Gentry 3751
Palmer 4; 819 (TYPE: *D. diffusa*)
Rose 16609
Wiggins 11409

D. GLANDULOSA Presl

Carter et al. 2379; 2447
Carter & Ferris 3774; 3907
Jones, M. E. 24149; 24190; 24191; 27050 (TYPE: *D. fendleri* var. *perennis*)
Purpus 469

D. GRACILIS ssp. CARINATA (Brandegee) J. Duke

Brandegee 34 (TYPE)
Gentry 4415 (TYPE: *D. carinata* var. *perennis*)
Jones, M. E. 24193
Purpus 216

D. HOLOSTEOIDES Benth.

Bryant 1888 (TYPE: *D. veatchii*)
Carter et al. 1935; 2474
Carter & Kellogg 3089; 3221
Chambers 837
Constance 3135
Gentry 4059; 7516
Hinds s. n. (TYPE)
Johnston 3048; 3949; 4263
Jones, M. E. 24076
Mason 1908
Palmer 570
Purpus 151
Reed 6156; 6255
Rose 16268; 16528
Shreve 7053; 7095
Wiggins 5456; 5531; 7898; 11350

D. HOLOSTEOIDES var. CRASSIFOLIA (Benth.) J. Duke

Carter et al. 2255

Constance 3185
Craig 726
Hinds s. n. (TYPE)
Howell 10572
Jones, M. E. 27046
Moran 4168
Xantus 6

D. LEPTOPHYLLA (Cham. & Schlecht.) Fenzl. ex Rohrb.

Wiggins & Demaree 4915

D. VISCOSA S. Watson

Dressler 599
Gentry 7359
Orcutt 51; 1330 (TYPE)
Palmer 767
Shreve 6950
Wiggins 7862

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D. CORDATA (L.) Willd.

Aguilar 193; 978
Calderón 266
Carlson 831
Chaves 319
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Gentle 3028
Glassman 1805
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Mitchell 47
Muenscher 12352; 12475
Oersted 3640; 3649
Orozco 434; 436
Peck 519
Rodríguez, J. V. 2196
Rowlee & Rowlee 345; 500
Standley 1720; 2300; 7691; 8588; 8921; 17158; 17541; 19236; 20236; 21557; 22502; 22650; 22714; 23493; 24022; 44268; 53336; 66994; 72489; 75828; 76914; 87923; 88760; 89508
Standley & Elías 2542; 2687
Standley & Jaime 5633; 7197
Steyermark 38793; 47853
Stork 8; 1065
Tonduz 11431
Valerio 187
Velasco 8893
von Wedel 1249A
Watson 20
Wilson 554
Yuncker 4770

D. EFFUSA var. DEPRESSA (Greene) J. Duke

Steyermark 50243 (TYPE: *D. minuscula*)

D. GLANDULOSA Presl

Bernoulli 240 (TYPE: *D. leptoclados*)
Standley 58053; 59111; 59852; 60343; 60837; 60874; 60893; 61235; 62818; 62897; 63790; 64317 p. p.; 64427; 66095; 66170; 67287; 77390; 80085; 80810; 81211; 81909; 82454; 83002; 83193; 83247; 83512; 83884; 84704; 85793
Steyermark 32299; 33991

D. LADEWII Rusby

Heyde & Lux 4444
Hunnewell 14660
Nelson 3706
Stanley 58398; 59961; 61978; 65477; 67942; 68554; 80175; 80683; 83275; 83294; 83823; 85147; 85599; 85827; 86254
Steyermark 30047; 32349; 33964; 35653; 36187

D. LAXIFLORA Benth.

Bernoulli & Cario 3255
Hartweg 523 (TYPE)
Steyermark 35768

D. MULTIFLORA Brandegee

Bell & Duke 16975
Skutch 2992
Standley 59446; 65172; 79941; 80208
Steyermark 30500

D. VILLOSA Cham. & Schlecht.

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Bell & Duke 16971
Bernoulli 18
Brenes 5765; 17202; 17415
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Glassman 2049
Heyde & Lux 3084
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Johnston 104
Kellerman 7625; 8013
Molina 337
Morales 1245
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Standley, Allen et al. 919
Standley & Elías 2533
Standley & Jaime 6748; 6926 p. p.
Standley & Lindelie 7469
Standley, Williams et al. 1225
Steyermark 29615; 29910; 35044 p. p.; 50528
Tonduz 749
von Tuerckheim 684 (appr. *D. malachioides*)
Williams & Molina 10076; 12016
Woodson, Allen & Seibert 1162; 1771 p. p.
Woodson & Schery 710
Yuncker, Dawson & Youse 5856

D. VILLOSA ssp. PALUSTRIS (Cham. & Schlecht.) J. Duke

Muenscher 12428
Skutch 298
Standley 61036; 61054; 61553; 62663; 62855; 62969; 64316; 64697; 64709; 65915; 67816; 82677; 83746; 85203; 85816; 87192
Standley & Elías 3170; 3649
Standley & Jaime 5503
Steyermark 34454; 35044 p. p.; 35597; 35735; 50126; 50314

WEST INDIES

D. CORDATA (L.) Willd.

Baker 1375
Baker & van Hermann 4246
Boldingh 1670; 2306
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Britton 2287; 3303
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Ekman 612; 9469; 12798 (TYPE: *D. adenophora*); 13871
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Harris 8444; 11704; 12760
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Howard 6557; 10625
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Hunnewell 15267; 19453
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Leonard 8347; 9217
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Wight 99
Wilson 1166
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Wright 24
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D. ORTEGIOIDES Griseb.

Britton, Britton & Wilson 14279
Curtiss 397
Wright 2019 (TYPE)

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D. CORDATA (L.) Willd.
Bonpland 222
Broadway 575
Farenholtz 554; 665 (var. *pacifica*)
Fendler 48
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D. FIRMULA Steyermark
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D. VILLOSA Cham. & Schlecht.
Farenholtz 795
Pittier 12672

D. VILLOSA ssp. PARAMORUM (S. F. Blake) J. Duke
Jahn 111 (TYPE)
Pittier 13170

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D. CORDATA (L.) Willd.
André 747 (p. p.)
Allen, C. 468
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Fosberg 19276; 19491, 20367
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Killip & Smith 17425 (aber.)
Lehmann 5997 (var. *pacifica*)
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Toro 15
Triana s. n. (TYPE: var. *puberula*)
von Sneidern 2256

D. GLANDULOSA Presl
Apollinaire 24

D. OVATA Humb. & Bonpl. ex Roem. & Schult.
André 747 p. p.; 2778; 5865; 6112; 6384
Arbeláez & Cuatrecasas 6001
Pennell 7133; 7139; 7621; 8914
Rusby & Pennell 622

D. VILLOSA Cham. & Schlecht.
André 4289 (appr. ssp. *palustris*)
Arbeláez & Cuatrecasas 5260
Killip & Smith 16142 p. p.; 17073
Pennell 1733; 3244
Smith, H. H. 556 (appr. ssp. *palustris*); 2830

D. VILLOSA ssp. PALUSTRIS (Cham. & Schlecht.) J. Duke
Killip 5358 p. p.; 6732
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D. VILLOSA ssp. PARAMORUM (S. F. Blake) J. Duke
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D. CORDATA (L.) Willd.
Eggers 14659; 15170 (var. *pacifica*)
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D. OVATA Humb. & Bonpl. ex Roem. & Schult.
André 3653
Benoist 2367 (aber.)
Camp 2576; 2620
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Fosberg & Prieto 22689 p. p.; 22789
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Tate 559; 595; 610
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D. ROTUNDIFOLIA var. NITIDA (J. Ball) J. Duke
André 3978 (appr. *D. glaberrima*)

D. STELLARIOIDES Humb. & Bonpl. ex Roem. & Schult.
Camp E-1862
Fosberg 23203
Hitchcock 21406
Jameson 100
Pachano 95
Rose, Pachano & Rose 22952; 23183 p. p.
Rose & Rose 22805

D. VILLOSA Cham. & Schlecht.
André 1988

D. VILLOSA ssp. PALUSTRIS (Cham. & Schlecht.) J. Duke
Benoist 77
Camp E-1929; E-2624
Fosberg & Prieto 22689 p. p.
Rose, Pachano & Rose 23183 p. p.; 23875 p. p.

Galapagos Islands

D. cordata (L.) Willd.
Baur 3
Howell 9158; 9671
Stewart 1513; 1514; 1515; 1516; 1517
Svenson 65 (type: var. *pacifica*); 134 (var. *pacifica*)

D. monticola Howell
Bowman 77
Howell 9243 (type)

D. rotundifolia A. Gray
Stewart 1512 (var. *nitida* ???)

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D. apetala Bartl.
Pavón s. n. (type: *D. virgata*)
Pennell 14321
Soukup 2823
Weberbauer 5814; 5827
Wilkes Exped. s. n. (type: *D. macrantha*)

D. auriculipetala Mattf.
MacBride & Featherstone 2264 (type)

D. cordata (L.) Willd.
Gay 899
Ferreyra 255; 1064; 1758; 11305; 12726; 12753
Hunnewell 15972
MacBride 3918
Nuñez, O. V. 727
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D. divaricata HBK?
Ferreyra 3460
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D. divaricata var. divergens J. Duke
Asplund, E. 13731
Ferreyra 1724
Nuñez 2320, 4189 p. p.

D. divaricata var. reflexiflora J. Duke
Ferreyra 3855 p. p.; 3958; 8695a; 11522
Nuñez 2261; 3579; 3754; 3752; 3755; 3757; 3758; 4198; 4291

D. divaricata var. stricta (Rusby) J. Duke
Ferreyra 763 (appr. *D. glaberrima*); 1497
Lechler 1947 (type: *D. agapatensis*)
Weberbauer 5327 (appr. *D. glaberrima*)

D. divaricata var. viscidula (A. Gray) J. Duke
Ferreyra 6102
MacBride & Featherstone 189?
Pennell 14518, 14516
Stork 11456
Weberbauer 10143
Wilkes Exped. s. n. (type)

D. engleriana (Muschl.) Baehni & MacBride
Cerrate 1583; 3384
Weberbauer 3101 (type)

D. engleriana var. devia (Baehni & MacBride) J. Duke
MacBride & Featherstone 566
Pennell 13462; 14655 (type)
Tovar 1277B

D. fasciculata A. Gray
Cerrate 621; 3092
Ferreyra 7422
MacBride & Featherstone 187 (appr. *D. glandulosa*); 693
Pennell 14515
Wilkes Exped. s. n. (type)

D. frutescens Mattf.
Weberbauer 7203 (type)

D. glaberrima Bartl.
Haenke s. n. (type)
MacBride 3506
Woytkowski 34228 (???)

D. grandiflora Bartl.
Cerrate 1101
Ferreyra 6245; 8587 (appr. *D. glaberrima*)
Pennell 14724
Vargas 1903

D. ovata Humb. & Bonpl. ex Roem. & Schult.)
Espinosa 199
MacBride & Featherstone 1714

D. paposana Phil.
Nuñez 4189 p. p.; 2430 (appr. var. *weberbaueri*)

D. paposana var. weberbaueri (Muschl.) J. Duke
Cerrate 860
Ferreyra 1398; 2435; 3855; 6328 p. p.; 8025; 8695; 9580
Grant 7441, 7468

MacBride 5863, 5904 (aber.) 5963
Miranda 0367
Pennell 14783
Soukup 2111
Stork, Horton & Vargas 9241
Stork & Vargas 9357
Weberbauer 1657
Worth & Morrison 15741 (appr. var. *paposana*)

D. PAPOSANA var. SERRULATA J. Duke
Ferreyra 1497; 1515; 7234; 8816; 11616; 13428; 13490; 13522
Matthews 997
Worth & Morrison 15677

D. PRAECOX Baehni & MacBride
Weberbauer 6916 (TYPE)

D. ROTUNDIFOLIA A. Gray
Ferreyra 647; 6949; 7048; 8301
Killip & Smith 21761
MacBride & Featherstone 183; 261
Pennell 14390; 14516 p. p.
Savatier 373
Weberbauer 7397
Wilkes Exped. s. n. (TYPE)

D. ROTUNDIFOLIA var. NITIDA (J. Ball) J. Duke
Ball, J. s. n. in 1882 (TYPE)
Balls, E. K. 6789
Cerrate 150; 627; 1376
Cook & Gilbert 615; 638
Ferreyra 3030 (appr. *D. glaberrima*); 7428
Killip & Smith 21810
MacBride 3506 (appr. *D. glaberrima*)
MacBride & Featherstone 188 (appr. *D. cordata*)
Nuñez 1313
Savatier, L. 372
Stafford s. n. (closely resembles Ball s. n. from Chicla)

D. STEREOPHYLLA Mattf.
Balls, E. K. 7021, B7021
Goodspeed, Stork & Horton 11533
Killip & Smith 22132; 22134
MacBride & Featherstone 563; 962 (TYPE); 1761
Rose & Rose 18718
Stork 10925
Tovar 220
Weberbauer 6600 (TYPE: var. *exstipulata*)

D. VILLOSA Cham. & Schlecht.
Haenke s. n. (TYPE: *D. hirsuta*)
Killip & Smith 23212
MacBride 3266
MacBride & Featherstone 1543
Poeppig 1575
Vargas 2100

D. VILLOSA ssp. PALUSTRIS (Cham. & Schlecht.) J. Duke
Allard 21093
MacBride 4835
MacBride & Featherstone 1542 (TYPE: *D. sphagnophila*)
Stork & Horton 10479

BOLIVIA

D. CORDATA (L.) Willd.
Bang 233
Buchtien 183 p. p. 255; 5405
Krukoff 10401
Rusby 1182
Steinbach 1922; 5442; 6216; 6269
Weddell 4591
Williams 56

D. DIVARICATA var. STRICTA (Rusby) J. Duke
Tate 160 (TYPE)

D. GLANDULOSA Presl
Bang 92 (appr. *D. cordata*); 1136
Buchtien 572
Cárdenas 609a; 2424
Eyerdam 24941; 24957
Fiebrig 2837
Hammarlund 404
Mandon 950
d'Orbigny 1187
Steinbach 4011

D. LADEWII Rusby
Tate 652 (TYPE)

D. OVATA Humb. & Bonpl. ex Roem. & Schult.
Cárdenas 2332; 3379
Herzog 2390

D. ROTUNDIFOLIA var. NITIDA (J. Ball) J. Duke
Mandon 948 (appr. *D. ovata*)

D. VILLOSA Cham. & Schlecht.
Buchtien 183 p. p.
Mandon 949
Tate 928

D. VILLOSA ssp. PALUSTRIS (Cham. & Schlecht.) J. Duke
Rusby 1183

Chile

D. papposana Phil.
Jaffuel 1025; 1033 (appr. *D. rotundifolia*); 2549
Johnston 3620; 5213

Paraguay and Uruguay

D. cordata (L.) Willd.
Balansa 2273; 4586
Bartlett 21026
Jorgenson 4016

The Guianas

D. cordata (L.) Willd.
Berthaud-Caulon 538
Broadway 27
Focke 302
Hering & Dieperink 113
Hostmann 714a
Maguire & Fanshawe 23562
Mell 232
Persaud 165
Schomburgk 930
Sieber 392

Brazil

D. cordata (L.) Willd.
Baduin, J. 3090
Barreto, M. 1418
Blanchet 208; 1218
Burchell 1011; 9710-2; 10071
Dusen 6667; 14165
Gardner 317
Glaziou 5746
Irwin 2184
Klein 443
Leite 523; 3937
Mosen 409
Muller 249
Netto 124
Pickel 2737
Piers & Black 632
Puiggari 2936
Reineck & Czermak 47
Riedel 704; 790
de Sampaio 1579; 1964
Segadas-Vianna 2642
Splitgerber 216
Spruce 216
Smith & Reitz 8799

Argentina

D. cordata (L.) Willd.
Budin 14001
Burkart 7276
Lorentz & Hieronymus 1123
Parodi 9080
Venturi 5104; (var. *pacifica*); 5911; 8018
Jorgensen 1172
Parodi 8038
Pierotti, S. A. 1994
Schreiter 10960
Schulz 977
Venturi 3685; 9430

D. glandulosa Presl
Eyerdam & Beetle 22360
Hieronymus 233

D. ovata Humb. & Bonpl. ex Roem. & Schult.
Venturi 2900; 4421

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D. cordata (L.) Willd.
Backer 10294, 32379, 32380 (all var. *pacifica*); 8642 (appr. *D. diandra*)
Bakhuizen 28a (var. *pacifica*)
Buchtien 695, 795 (var. *pacifica*)
Bunnemeyer 11072
Cid 20 (var. *pacifica*)
Dames 85
Degener 12345 (var. *pacifica*)
Edaño 1480, 11845 (both var. *pacifica*)
Flecker 3184
Heller 2639
Hochreutiner 106, 1090
Kakah 53 (var. *pacifica*)
Koorders 16539b; 16540b; 43293b (all var. *pacifica*)

Meebold 21805 (var. *pacifica*)
Nodi & Idjan 253
Nur, Md. 34319
Ottolander 246 (var. *pacifica* appr. ssp. *diandra*)
Posthumus 3459 (var. *pacifica*)
Purseglove 4322 (var. *pacifica*)
Schiffner 1956; 1958; 1960; 1961 (var. *pacifica*)
St. John 9938
St John & Catto 17850
Steiner 34787
Topping 2999
Van Royen 4312
Womersley & Van Royen 5911 (var. *pacifica*)
Womersley, Hoogland & Taylor 4909 (var. *pacifica*)

D. CORDATA ssp. DIANDRA (Blume) J. Duke
Balapur 570
Biswas 4445
Bloembergen 3371
Bodinier 361
Boeea 8482; 8653; 8921
Bon 5837
Boswezen 3065; 3317
Brass 3784; 13237; 23827
Carr 11932
Chevalier 29323
Chun & Tso 44268
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Clemens 17642; 41187
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Evtard 215
Eyma 1139
Floyd & Hoogland 4006
Forbes 3910
Galoengi 95
Gjellerup 1100
Gressitt 297
Griffith 339
Hoogland & Pullen 5293
Jacquemont 1523
Kajewski 2176
Kalkman 4526
Kanehira & Hatusima 13422
Kaudern 168
Kerr 2409
Kobayasi 397
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SANANGO: NEW AMAZONIAN GENUS OF LOGANIACEAE

GEORGE S. BUNTING AND JAMES A. DUKE

ABSTRACT

The new genus, **Sanango**, shows affinity to the genera *Buddleja*, *Nuxia* and *Peltanthera*, of the Loganiaceae, though the five-lobed corolla with only four stamens is more characteristic of other families, such as the Scrophulariaceae. Various features of **Sanango durum** are discussed and illustrated. GEORGE S. BUNTING, L. H. Bailey Hortorium, Cornell University, Ithaca, New York; JAMES A. DUKE, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

Among recent collections of Felix Woytkowski from Amazonian Peru is a specimen of a plant that appears to be intermediate between the families Loganiaceae and Scrophulariaceae! It is a fine example of the situation which has led to the widespread view that the Loganiaceae are an artificial group constituted primarily of genera excluded for one reason or another from other well-marked, natural families. There is still ample cause to argue this case, for there is no obvious "family resemblance" to guide us, and often the circumscription of the family is inadequate to positively include or exclude an unknown plant.

A century ago George Bentham (Jour. Linn. Soc. Bot. 1:52–114. 1854) wrote: "There can be no doubt that Rubiaceae, Apocyneae, Gentianeae, and Scrophularineae are large independent orders indicated in nature, yet those genera now amalgamated under the name of Loganiaceae bind them so firmly together, that some of these genera will be found even more closely allied to certain others of each of the above orders respectively than they are to each other." And he continues: "The Loganiaceae lie very near to some part or other of the vast family of Rubiaceae, but by their free ovary, they are absolutely, and by very few exceptions, clearly separated. The connecting genera with the Apocyneae, Gentianeae, and Scrophularineae are on the other hand, much fewer, but their union is much closer. With Scrophularineae in particular, although the general affinity is more remote, the few intermediate genera and species are intermediate in every respect, in habit as in technical characters. The main distinction, the presence of stipules in Loganiaceae, disappears very gradually, and the difficulty of drawing the line is the greater from there being no habit or family resemblance to unite the several members of the Loganiaceae."

It is in this paper that Bentham discussed the similarity of the genus *Buddleja* (previously included in Scrophulariaceae) to *Logania*, and concluded the necessity to place them together, along with the genus *Polypremum*, in the family Loganiaceae.

Now we have discovered another plant that seems to stand nearly between the Loganiaceae and Scrophulariaceae. The fruiting specimen has a distinct aspect of *Buddleja*, but several technical features prevent its inclusion in that genus. It is equally, if remotely, allied to the genus *Peltanthera*. After thorough study of this plant, and consultation with N. Y. Sandwith at Kew, and J. J. Wurdack at Washington, we are convinced that it represents an unnamed genus, and describe it as new.

Issued December 28, 1961

Sanango Bunting et Duke, gen. nov.

Arbores parvae ligno valde duro, foliis oppositis petiolatis binis lineis conjunctis. Flores in thyrsis bracteolatis, calyce ad medium lobato, segmentis lanceolatis subaequalibus, corolla 5-lobata, ± hypocrateriformi, gibbosa, segmentis rotundatis subaequalibus, aestivatione cochleari, staminibus 4 (!) sub sinibus prope tubi basim affixis, filamentis inflatis, antheris subrotundis singulatim 2-thecas ferentibus, introrsis versatilibus in linea ± hippocrepiformi aperientibus, staminodio parvulo, ovario globoso leviter 4-lobato biloculari disco cupuliformi circumdato placentis axillaribus multiovulatis, stylo brevissimo, stigmate capitato bilobato. Capsula polysperma septicidalis, utroque carpello iterum scisso.

Sanango durum Bunting et Duke, sp. nov.

Arbor 16 m. alta ramulis lenticellatis. Foliorum lamina 10–25 cm. longa 4–7 cm. lata elliptica vel anguste obovata ad apicem acuminata, ad basim cuneata vel attenuata, parce et inaequaliter denticulata praecipue in dimidio superiore, venis lateralibus utrinque 5–7 arcuatis ascendentibus, infra pallida venis strigulosis instructa; petiolus 0.5–1.0 cm. longus, ad basim latus, facie adaxiali velutina ferruginea. Inflorescentia 5–12 cm. longa terminalis vel axillaris ± secunda, pedunculo et pedicellis strigulosis, pedicello ca. 1 mm. longo; florum calyces ca. 3.5 mm. longi puberuli lobis 5 acutis 1.5–2 mm. longis; corollae albae aliquantum carnosae, ca. 1.2 cm. longae extus puberulae et glanduloso-puberulae, intus glanduloso-puberulae et etiam pilosae in tubi basi, lobis ca. 3–4 mm. longis; filamentorum staminalium partes liberae pilulosae vix 2.5 mm. longae antheris ca. 0.5 mm. latis brevioribus quam latis; staminodium parvulum vix 0.2 mm. longum; ovarium globosum ca. 1 mm. longum, disco cupuliformi tam procero atque ovario; stylus crassus persistens, una cum stigmate magno ca. 1 mm. longus. Capsula ellipsoidea vel anguste obovoidea ca. 3.5–4.0 mm. lata parietibus osseis; semina orthotropa ± elongata fusiformia ca. 0.7 mm. longa recta vel sigmoidea.

Type collection: *Felix Woytkowski 5619*, "tree 12 m. tall; no latex; flowers white; in forest, elev. 300 m.; Aramango, s. of Nazaret," depto. Amazonas, Peru; 2 April 1960 (HOLOTYPE MO, isotype K, US).

Distribution: Forests between 300 and 750 m. elevation, west central Amazonas and central Junín, Peru. These localities are separated by nearly 500 air miles. It seems plausible that the distribution may be more or less continuous between these points.

PERU: Junín: Satipo, Aug. 1960, *Woytkowski 5925* (MO).

Vernacular name: "Sanango" (Amazonas).

The generic name *Sanango* is the colloquial name furnished by the collector of this plant. It is a corruption of a Quechuan word, "sanangu", an Indian word applied also to species of *Tabernaemontana*, *Rauwolfia*, and *Malpighia*. The specific epithet refers to the hard wood to which Woytkowski called attention in his field notes. Untreated, the wood disfigures a razor blade when one attempts to cut a hand section.

Figure 1. *Sanango durum* Bunting & Duke. a. flowering branch b. flower c. flower with corolla cut open d. stamen from young flower bud, with adaxial view of young anther (center) and anther after dehiscence (top) e. enlargement of pistil, ovary nearly covered by cup-like disk f. diagrams of a single flower bud from opposite sides illustrating aestivation. g. seed

Sanango belongs to the subfamily Buddlejoideae. Its nearest relatives appear to be *Buddleja*, *Nuxia*, and *Peltanthera*. It should be noted that *Sanango* has been collected only in localities that lie in the middle of the known range of *Peltanthera*.[1] Although the affiinity is not strong, these latter two genera share the following characteristics: hippocrepiform dehiscence of the anthers, a disk between the ovary and corolla, multicellular hairs, and a lack of stipules.

The combination of characters occurring in *Sanango* is unusual in Loganiaceae, but most of them occur singly in some other genus of the family. The hippocrepiform mode of dehiscence of the stamens occurs also in the African genus *Nuxia*.

There is a very well developed annular disk of firm texture in the flower of *Sanango*. In *Peltanthera*, a very short disk is present, conspicuous only in young flowers. In *Nuxia*, however, the disk is annular, and though membranous, very similar in form to that in *Sanango*.[2] Notwithstanding, the style and stigma of each of these three genera are extremely different.

An approach to the *Sanango*-type pistil occurs in *Buddleja*, and in the herbaceous genera *Mitreola* and *Polypremum*. In *Mitreola*, the style is short, the stigma smaller than in *Sanango*, and the ovary splits in two at the top as it develops. Even more similar is the fruit of *Polypremum* which splits into four segments at maturity as it does also in *Buddleja*.

Multicellular hairs similar to the dendroid or branched type in *Peltanthera* have not been observed in *Sanango*, nor have we encountered the glandular, peltate type similar to those described by Solereder (Pflanzenfam. $4^{(2)}$:23, *fig. 12*. 1892) and by Hunziker and Fulvio (op. cit. in footnote). Certain types of multicellular hairs are, however, common in *Sanango* on both vegetative and floral parts.

The corolla is 5-lobed in some genera of Loganiaceae and 4-lobed in others. Indeed both conditions are known to exist in a single species of *Buddleja*. The loganiaceous flower typically has an equal number of stamens and corolla lobes. *Sanango* is unique[3] in the Loganiaceae in possessing a five-lobed corolla with only four stamens, the fifth one merely suggested by a very small appendage not apparent in all flowers. This characteristic is typical of such families as Verbenaceae and Scrophulariaceae. We feel, nonetheless, that *Sanango* is more closely allied to Loganiaceae than to any other. Such an opinion is dictated by the presence of a stipular line between the leaf bases of each leaf pair, and the strong similarity of the pistil and the fruits to *Buddleja*, which clearly is related to *Logania*. The more or less irregular nature of the corolla in aestivation, and the reduction of one stamen in *Sanango* decidedly suggest Scrophulariaceae. There is,

---

[1] In their excellent paper on *Peltanthera*, Hunziker and Fulvio (Bol. Acad. Nac. Ci. Cordoba 40: 217–228. 1957) noted that the genus is known from Costa Rica, Peru, and Bolivia. During the course of this study we have encountered the collection of A. E. Lawrence (no. 432; ca. 100 mi. n.w. of Bogota, depto. Boyaca, Colombia) which clearly represents *P. floribunda* Benth. as circumscribed in that paper. The Colombian specimen agrees in all its floral measurements with those cited by Hunziker and Fulvio for Costa Rican specimens, with the exception of the placentae which seem to extend at least half the length of the ovary as is characteristic of the Bolivian specimen.

[2] The ovary of *Nuxia floribunda* Benth. is deeply two-lobed, which, surrounded by the annular disk, is very suggestive of *Rauwolfia* and other Apocynaceae.

[3] In the African genus *Usteria*, three of the four stamens regularly abort.

however, no tendency toward didynamy of the stamens, as is characteristic of the latter group.

Aestivation

Aestivation of the flowers of this genus is cochlear, i.e., one corolla lobe is interior, one exterior, and the other three have one edge overlapping and exposed with the opposite edge hidden by the adjacent overlapping lobe (Fig. 1f). The corolla tube is gibbous near the base, and the flower appears to be oriented so that the interior corolla lobe and the gibbous side of the tube are uppermost (adaxial). The vestigial fifth stamen arises on the gibbous side, below one of the two sinuses adjacent to the interior corolla lobe (Fig. 1c). The bud is distinctly zygomorphic, more so than in *Peltanthera*. It is impossible to ascertain from the dried material to what degree the open flower may show this character.

We are unaware of an identical type of aestivation among the other Loganiaceae, though it is not uncommon among the dicots. The usual pattern in five-lobed corollas of this family is with two lobes external, two internal, and one imbricate.

Vesture

At least four types of multicellular hairs occur in *Sanango*. The largest are present on the adaxial face of the basal part of the petiole. These are composed of 3–5 elongate, hyaline cells, the basal one inflated, the terminal one attenuate (Plate IVa). Very young stems and leaves are clothed with hairs of a similar type, a few of which persist on the veins on the lower surface of the mature leaves.

The calyx bears hairs of similar structure, but very much smaller than those described above. In some, however, it appears that the terminal cell is slightly inflated (Plate IVb).

Both surfaces of the corolla are very hairy (Plate IVc). The outside is closely covered by very small, mostly 3-celled attenuate hairs similar in form to those of the leaves, and intermixed with these are some still shorter gland-tipped hairs (Plate IVe). The glandular tip cell is opaque, borne upon a greatly inflated, hyaline basal cell.

The inside of the corolla bears 3–4-celled, gland-tipped hairs about twice as long as those on the outside of the corolla (Plate IVc). [The glandular tip may be composed of several cells arranged radially, but the small size of the structure has prevented us from ascertaining its exact nature. Some lobing is apparent in certain preparations.] In addition, there are many very long, slender hairs in the throat of the corolla that appear to have no cross walls dividing them into cells (Plate IVd).

Pollen

A pollen sample was sent to Dr. G. Erdtman for study. He reports that "the grains are small, uninteresting from a morphological point of view, and similar to those in *Peltanthera* . . ." His diagnosis follows: "Pollen grains small, 3-colporate (about 15 × 12.5). Colpi about 12 μ long. Ora about 2.5–3 μ high. Exine thin. Sexine of about the same thickness as nexine. [No pattern or traces of bacula etc. could be seen even by means of an apochromatic objective with the numerical

aperture 1.40. The pollen grains in *Peltanthera costaricensis* are equally 3-colporate and measure about 15 × 11 μ; the exine seems to be very minutely reticulate.]"

Anatomical Considerations

Dr. Stern, U. S. National Museum, plans to do a detailed anatomical study of the wood of this genus. We wish, however, to point out that there appears to be no included phloem in this species, which is the typical condition in the Buddlejoideae. This contrasts strongly with the intraxylary phloem present in members of the Loganioideae (Metcalfe and Chalk 2:931. 1950). The wood does not appear to differ strikingly from that of *Peltanthera*.

Explanation of Plate

PLATE IV

Types of trichomes in *Sanango*

a. from adaxial face of petiole b. on calyx c. on corolla, exterior (left) and interior (right) [a–c all at same scale] d. enlargement of long hair on interior of corolla, a single short gland-tipped one at its base (note the apparent lobing of the glandular tip) e. enlargement of a single gland-tipped hair on exterior of corolla

BUNTING & DUKE—SANANGO

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TWO NEW MEMBERS OF THE GENUS SCOLECOPTERIS[1]

R. BRADLEY EWART

ABSTRACT

The genera of Carboniferous Marattiaceae are reviewed with special reference to *Scolecopteris*, and two new species of *Scolecopteris* are described: S. **monothrix** and S. **illinoensis**. *Scolecopteris monothrix* is unique in the long multicellular hair borne by each sporangium, while S. *illinoensis* is characterized by having five or six sporangia per synangium, small spores and conspicuous multicellular hairs on the lower surfaces of the rachis and pinnules. R. BRADLEY EWART, 228 Ridge Terrace, Park Ridge, Illinois.

INTRODUCTION

The genus *Scolecopteris*, founded by Zenker in 1837, is based upon silicified fructifications from the Lower Permian of Saxony. To date the following species have been described:

S. *elegans* Zenker, Linnaea 11:509. 1837. (A more detailed description was given by Strassburger in 1874.)
S. *subelegans* Grand'Eury, Acad. Sci. Inst. France, Mém. 24:72–73. 1877.
S. *ripageriensis* Grand'Eury, ibid., p. 73.
S. *minor* Hoskins, Bot. Gaz. 82:427–436. 1926.
S. *oliveri* Scott, Journ. Linnean Soc. London, Botany, 49:1–12. 1932, and pp. 309–321. 1933.
S. *latifolia* Graham, Bot. Gaz. 95:456–458. 1934. Emend Mamay, Ann. Missouri Bot. Gard. 37:425–428. 1950.
S. *radforthii* Andrews, Ann. Missouri Bot. Gard. 30:435–437. 1947.
S. *iowensis* Mamay, Ann. Missouri Bot. Gard. 37:429–431. 1950.
S. *minor* Hoskins, var. *parvifolia* Mamay, ibid., pp. 431–432.
S. *incisifolia* Mamay, ibid., pp. 433–436.
S. *major* Mamay, ibid., pp. 436–439.

Scolecopteris is characterized by pecopterid pinnules bearing sporangia in sori on the abaxial surfaces. The sporangia composing a sorus are attached to a common pedicel, but are free above, and lack a common synangial sheath.

The following account deals with two additional species that fit these characteristics and thus have been assigned to the genus *Scolecopteris*. Further evidence for placing them in this genus will be recorded under the description of each species.

[1] An investigation carried out in the graduate laboratory of the Henry Shaw Schoool of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Master of Arts.

Issued April 19, 1962.

MATERIALS

Both species are based on fertile pinnules found in coal balls that were collected by Dr. Henry N. Andrews from a site two miles northeast of Berryville, Illinois. The outcrop lies in the upper part of the McLeansboro group of the Pennsylvanian of Illinois.

THE CARBONIFEROUS MARATTIACEAE

Fructifications referable to the Marattiaceae are borne mostly on *Pecopteris* type foliage. They were borne on the under (abaxial) surface of the leaves, situated over a veinlet or between the veinlet tip and the margin, and unlike the living genera the majority of the fossils have radially symmetrical sori.

Mamay (1950) included the following genera in the Carboniferous Marattiaceae:

1. *Cyathotrachus* Watson, emend. Mamay: Synangia pedicellate; sporangia enclosed in a continuous synangial sheath; basal portion of synangium with central column; apical portion hollow and cup-like. Based on petrifactions.

2. *Ptychocarpus* Weiss: Synangia pedicellate; sporangia enclosed in a continuous synangial sheath, and fused to a central column extending through the entire length of the synangium. Based mainly on compressions.

3. *Scolecopteris* Zenker: Synangia pedicellate; sporangia attached to a central receptacle but free distally. Based mainly on petrifactions.

4. *Sturiella* Weiss: Synangia pedicellate; sporangia basally fused but free above; annulus present. Based mainly on petrifactions.

5. *Acitheca* Schimper: Synangia sessile; sporangia attached at their bases to a central column, with distal portions free; sporangial apices long and bristle-like. Based mainly on petrifactions.

6. *Asterotheca* Presl: Synangia sessile; sporangia attached to a receptacle, but free distally, their long axes parallel to the plane of the pinnule. Based mainly on compressions.

7. *Eoangiopteris* Mamay: Sori linear; sporangia arranged in two rows along fleshy receptacle; sori located along lateral veins; sporangia free. Monotypic. Based on petrifactions.

Thus, the accepted criteria for separating the fossil genera are the following:

1. Sori linear or radial.
2. Synangia pedicellate or sessile.
3. Sporangia free above or enclosed in a continuous synangial sheath.
4. Central column present or absent in synangia. (It is important whether the central column extends through the full length of the synangium or not, as in distinguishing *Cyathotrachus* from *Ptychocarpus*.)

Since the discovery of the pteridosperms, some paleobotanists have regarded certain of the supposed marattiaceous fructifications as more correctly referable to Pteridospermae. Kidston (1925) expressed this view in finding resemblances between *Acitheca* and *Telangium*. However, Mamay (1950) concluded that upon the basis of the sizes of fructifications and spores, the arrangement of sporangia in sori, and the superficial position of sori, this fossil group more closely resembles the living Marattiaceae than the pteridosperms.

Mamay (1950) considered the coenopterid fructification *Chorionopteris* to best fill the qualifications of a progenitor of the Marattiaceae. This evolution supposedly came about by means of a "phyletic slide" from marginal or terminal sori to superficial ones. He further proposed that those fossil genera with fused sporangia are most closely allied to the living genera *Danaea* and *Christensenia*, while those with free sporangia are most closely allied to the living genera, *Angiopteris*, *Archangiopteris*, and *Macroglossum*.

Description of New Species

Scolecopteris **monothrix** R. B. Ewart, sp. nov. (figs. 1–12).

This fructification is distinguished by long slender sporangia each of which terminates in a single, unbranched, multicellular hair. These were borne on pecopterid pinnules with strongly inflexed and deeply incised margins in synangia consisting of four, sometimes five, or rarely three sporangia.

One well-preserved specimen was discovered in coal ball WCB 1203. It consists of an ultimate rachis with about 15 attached pinnules. Several detached pinnules and synangia were found in the same coal ball. A second intact specimen was found in WCB 1238 along with more fragments.

Nearly all synangia were found attached to pinnules and seem to have been preserved in their natural position. The morphology of the ultimate rachis and attached pinnules may be seen in the reconstruction in text-fig. 1.

The average dimension of the pinnules and penultimate mid-rib are as follows:

Pinnule length (normal)	6.0 mm.
Pinnule length if unrolled	12.0 mm.
Pinnule width (normal)	2.5 mm.
Pinnule width if unrolled	10.5 mm.
Penultimate midrib diameter	0.85 mm.

The penultimate or rachis midrib (fig. 7) shows no cellular detail except for the vascular supply which consists of a U-shaped strand with the concavity adaxial. The basal part is two or three tracheids in width while the arms narrow to one tracheid. Short multicellular hairs are found on the lower side. Figure 11 (A) shows some of these hairs on the longitudinally sectioned midrib. Some of them are as long as the diameter of the midrib. Figure 7 shows that these hairs are several cells in width and are irregularly spaced in contrast to the hairs found in the sporangia.

As seen in fig. 11, the pinnules are joined laterally where attached to the rachis but become separate a short distance out from the rachis. They are of the pecopterid outline characteristic of the genus. The margins are so strongly flexed downward that they parallel and finally almost enclose the synangia as may be seen in fig. 10 (B). The pinnule is devoid of synangia along the distal third of its length and this portion is strongly flexed downward and inward toward the rachis midrib almost completely enclosing the synangia and the space directly below them. This space appears to be loosely filled with sporangial hairs which are oriented in the direction of the midrib. These hairs may be seen, mostly in transverse section, in

fig. 10 (A). The pinnule margins are deeply incised and may be compared in structure to those of *S. latifolia* and *S. incisifolia.* Figure 12 (B) shows one of the marginal lobes in vertical section. A row of these lobes in transverse section may be seen in figs. 8 and 11 (B). In fig. 8 the cellular contents of these lobes may be seen. The lobes join laterally at about the level of the sporangial apices, but their vascular strands continue as discrete bundles. The only other cellular structure of the lamina that is preserved is a layer of hypodermal cells below the upper epidermis; it is one or two cells in thickness and may be seen at the top of fig. 4 and in figs. 10, 11, and 12.

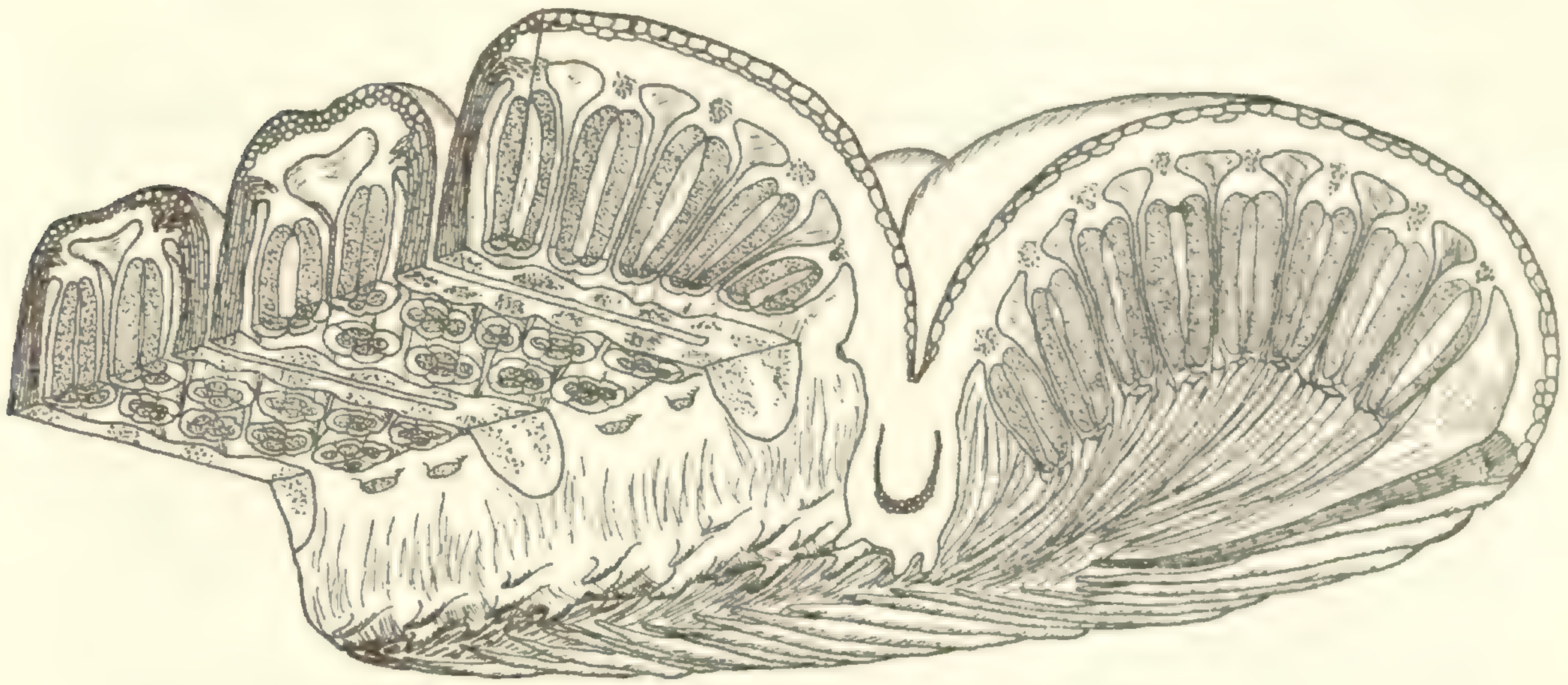
The synangia form a single row of nine or ten sori on either side of the midrib of each pinnule.

A synangium usually contains four sporangia, but those with five, such as the one in fig. 9, are also common and one has been found with three. The sporangia composing a synangium are arranged radially on a common pedicel. Due to the long slender nature of the synangia, it was not possible to find a good median longitudinal section showing both the pedicellate attachment and the apex bearing a portion of a sporangial hair. Thus, fig. 4 was prepared from three photomicrographs showing these features in their proper proportions: the upper shows the pedicellate attachment and the proximal half of two sporangia; the middle shows the distal half of two sporangia and their apices; and the third shows simply the basal portion of a hair characteristic of the species.

The sporangia are long, slender and roughly cylindrical but are slightly wider near the base than at the apex; they are tightly appressed to one another and the synangia themselves are quite crowded. The apex of each sporangium, prior to dehiscence, is curved inward toward the center of the synangium and fits closely against the apices of the other sporangia (figs. 2, 4). Thus a central synangial cavity is formed which is completely enclosed. Dehiscence was accomplished by a longitudinal slit along the inner face of the sporangium (fig. 1); in fig. 8 a mass of spores may be seen discharging through the slit.

This leads to the question of how the spores escaped from the enclosed synangial cavity. Figure 6 shows a synangium of *S. monothrix* at a later stage and is from a different specimen than that shown in most of the figures. The preservation is poor but it may be seen here that the sporangia have separated except where joined to the pedicel. This synangium, along with several empty ones, was attached to a fragment of a pinnule. In all probability the strongly curved pinnules to which these fructifications are attached straightened somewhat at maturity, decreasing the crowding of the synangia, and allowing the component sporangia to separate.

In figs. 3 and 4 it may be seen that a single, long multicellular hair is attached on the outer periphery of a sporangium near the apex. It is likely that such a hair grew on most if not all sporangia of *S. monothrix*, but no sporangium has been observed to have more than one hair. No branching has been observed in these hairs nor has any deviation in position or structure been noted. In fig. 3, the "bulb" at the distal end of the hair is merely the point at which the hair leaves the plane of the section and is not the termination of the hair; the total length is much greater than is shown. By following the course of a cluster of hairs it



Text-figure 1. Reconstruction showing abaxial view of part of a pinna of *Scolecopteris monothrix*. Portions of some pinnules are cut away to reveal arrangement of the fructifications. × 9.

is possible to estimate their length. The hairs in such a cluster all tend to point in one direction, toward the rachis midrib. In fig. 10 (A), a cluster of hairs may be seen in transverse section in the space below the sporangia. In fig. 12, clusters of hairs may be seen on either side of and pointing toward the rachis midrib (A) where they terminate. It is almost certain that these hairs originate on the sporangia, as no trace of an attachment has been observed elsewhere. It is thus concluded that the sporangial hairs are 2 or 3 times the length of the sporangia or 4 to 6 mm. in length.

The average dimensions of a synangium are as follows:

Total length of synangium (exclusive of hairs)	2.0 mm.
Total length of sporangium (exclusive of hair)	1.8 mm.
Maximum diameter of sporangium	0.35 mm.
Diameter of pedicel	0.35 mm.

The spores as shown in fig. 5 are monolete and bilateral with a length of 12 μ and a width of 9 μ. The smooth walls appear to be thick, but lack any markings of the exine, except where obviously due to damage. The only member of the genus with smaller spores is S. *elegans* with spores 10 μ in diameter. Using the method described by Radforth (1939), the average number of spores per sporangium is estimated at 9,000.

From the above description it may appear that S. *monothrix* has some rather striking characteristics for this genus. Some thought was given to the possibility of establishing a new genus but it was decided that this would not be necessary. The following are the reasons for placing this species in the genus *Scolecopteris*:

1. It seems most appropriate to refer it to the Marattiaceae on the basis of the nonindusial sori borne on the abaxial surface of pecopterid leaves.

2. The pedicellate, radial synangia limit it to *Scolecopteris*, *Ptychocarpus*, or *Cyathotrachus*.

3. Lack of a continuous synangial sheath and central column limit it to *Scolecopteris*.

4. It is borne on pinnules with a morphological structure similar to those of S. *latifolia* and S. *incisifolia* and is believed to be closely related to these species.

5. Although it has a closed synangial cavity at maturity, this opens at a later stage causing the synangia to assume a more scolecopterid appearance. Other members of the genus, such as S. *incisifolia*, also have closely appressed sporangia.

6. Although hairs of the S. *monothrix* type are unique for the genus, S. *major* is known to have multicellular hairs on the sporangia.

7. Although S. *monothrix* has small spores and large sporangia, they do not represent the extremes of the genus. As mentioned above, S. *elegans* has smaller spores, while S. *major* has sporangia from 0.3 mm. to 1.1 mm. longer than those of S. *monothrix*.

Scolecopteris monothrix may be differentiated from other members of the genus by the following characteristics:

1. No other member of the genus has a single, long, multicellular hair in a fixed position on the outer periphery of the apex of the sporangium. The synangial hairs of S. *major* are quite different.

2. S. *oliveri* and S. *incisifolia* are the only other species with bilateral spores. Of these two, only S. *incisifolia* compares to S. *monothrix* in having a smooth exine but the spores of the former are 22 × 14 μ while those of the latter are only 12 × 9 μ.

3. In sporangial length, S. *monothrix* is intermediate between S. *major*, which is 0.3 mm. to 1.1 mm. longer, and S. *oliveri*, which is 0.48 mm. to 0.40 mm. shorter. However, both of these species have a greater sporangial width than S. *monothrix*. The ratio of sporangial length to width is greater in S. *monthrix* than in any other member of the genus, being about 6:1.

4. The blunt connivent apices of S. *monothrix* further distinguish it from S. *major*, which has very acute apices.

The specific name S. *monothrix* is proposed in reference to the unique sporangial hairs.

Specific diagnosis: Synangia consisting of four, sometimes five, rarely three sporangia basally attached to a common pedicel. Sporangia 1.8 mm. in length and 0.35 mm. in width; apices blunt, connivent in synangia but separating after dehiscence; dehiscence by longitudinal clefts along inner sporangial wall. A single, unbranched, multicellular hair one cell in diameter located on the outer periphery of the apex of each sporangium, reaching a length two or three times the length of a sporangium. Pinnules averaging 6 mm. in length and 2.5 mm. in width (exclusive of inflexed margins), margins strongly inflexed and deeply incised, ultimate rachis with U-shaped vascular strand and thick multicellular hairs averaging 0.85 mm. in length. Spores monolete, averaging 12 μ long and 9 μ wide, with thick walls and smooth exines.

Age: McLeansboro Group, Upper Pennsylvanian.

Locality: Berryville, Illinois.

Holotype slides: Slides 2987–2995 (from WCB 1203).

SCOLECOPTERIS **illinoensis** R. B. Ewart, sp. nov. (figs. 13 and 15–26).

This description is based upon specimens from WCB 1204 and WCB 1239, particularly the latter from which the type slides were chosen. The fructifications in these coal balls were found to be in an excellent state of preservation. They were found attached to pinnules which were in turn attached to pinnae midribs. By cutting WCB 1239 in two planes, it was possible to obtain peels which revealed the morphology and something of the anatomy of the specimens.

Five or six sporangia are radially grouped on a short common pedicel to form a synangium. Of the 14 synangia seen in fig. 16, four contain six sporangia, seven contain five, while it is difficult to determine the numbers of the other three. Examination of other synangia has shown that those synangia with six sporangia are almost as numerous as those with five. As may be seen in fig. 16, the synangia form a single row on either side of the pinnule midrib. There are generally six or seven synangia per row. A vascular bundle branching from the pinnule midrib is found at the base of each synangium as seen in fig. 23 (C).

The outer sporangial walls are thick and curved as seen in fig. 16, but are composed of but one layer of cells. The lateral walls are thinner and straight, but do not touch one another, except in synangia which, like the one at the bottom left of fig. 16, contain spores and are probably less mature than the others. It is likely that the sporangia in a synangium separate as they mature, like those in S. *monothrix*. Dehiscence occurs by means of a longitudinal slit along the inner wall of each sporangium. Most of the sporangia seen in this study had already dehisced but a few may be seen to contain spores (fig. 22). The sporangia are roughly ovate in vertical section with acute apices that curve inward toward the center of the synangium as seen in fig. 23 (B). The sporangial cavity does not extend into the distal part of the apex. Figure 13 shows a transverse section through the apices of a synangium.

The average dimensions of the fructifications are as follows:

Total length of synangium	0.66 mm.
Total length of sporangium	0.65 mm.
Maximum diameter of sporangium	0.31 mm.
Diameter of pedicel	0.16 mm.

The spores are spherical in shape and have a crescent-shaped indentation in the exine at one point as indicated by the arrow in fig. 18. Examination of well preserved spores leads to the conclusion that this may be regarded as a natural and constant character. The diameter of the spores averages 15 μ.

The penultimate midrib may be seen in transverse section in fig. 23 (A). The vascular supply consists of a U-shaped line of tracheids, and extending from the free end on the right hand side is a small bundle of tracheids representing a pinnule trace just departing.

Figure 24 represents an oblique longitudinal section of the vascular supply in an ultimate pinnule. The arrow indicates a branch of this trace. Following the trace distally, it may be seen that this is one of six such branches each of which passes into the pedicel of a synangium. One of these traces may be seen in transverse section in fig. 23 (C).

The pecopterid pinnules are alternately spaced along the rachis midrib as may be seen in fig. 15. The pinnule margins are minutely toothed (fig. 17) and reflexed downward (figs. 19–22).

Following are the average dimensions of the rachis midribs and pinnules in these specimens:

Pinnule length	5.5 mm.
Pinnule width	2.2 mm.
Rachis midrib diameter	1.0 mm.

Figure 19 shows a row of pinnules, each with a pair of sori, arranged along a rachis midrib and sectioned transversely. At the extreme left is the rachis midrib in oblique section. The anatomy of the pinnules is well shown in fig. 20. The upper epidermis is not preserved, but the underlying, large hypodermal cells (A), form a layer one or two cells thick. Below this layer is a zone of palisade parenchyma (B), consisting of one or two layers of narrow, tightly-packed, elongated cells. Underlying this is the spongy parenchyma (C) of loosely-massed rounded cells, and numerous air chambers. Bounding this is the lower epidermis (D).

A notable feature of *Scolecopteris illinoensis* is the abundance of hairs on the lower surfaces of the pinnule midribs (figs. 24, 26). They are multicellular, unbranched, and one cell in diameter. Figure 21 shows that they extend beyond the apices of the sporangia. The hairs in transverse section may be seen between the two rows of synangia in fig. 16. Similar hairs have been observed attached to the synangial pedicel. In fig. 22, the arrow indicates a small outgrowth of the sporangial wall which may be the base of a hair, but these have not been seen on other sporangia.

S. *illinoensis* clearly belongs in this genus but differs from other members of the genus as follows:

1. The only other species in which it is not rare to find six sporangia in a synangium is S. *iowensis*. S. *minor* rarely has six, but a comparison of that species in fig. 14 with S. *illinoensis* shows a distinct difference in numbers of sporangia.

2. This species differs from S. *iowensis* which has spores measuring 65–80 μ in diameter, four times the diameter of those in S. *illinoensis*. S. *iowensis* sometimes has a double series of synangia on each side of the pinnule midrib, while this has not been observed in the present species.

3. Although multicellular hairs are sparingly present on the lower side of rachis and pinnules of S. *minor*, no species has hairs on the pinnules that are as conspicuous as in S. *illinoensis*.

Specific diagnosis: Synangia consisting of five or six sporangia basally attached to a common short pedicel. Sporangia 0.65 mm. in length and 0.31 mm. in width; apices acute and incurved; dehiscence by longitudinal cleft along the inner sporangial walls. Pinnules averaging 5.5 mm. in length and 2.2 mm. in width, with inflexed minutely toothed margins. Ultimate rachis with U-shaped vascular strand. Unbranched, multicellular hairs, one cell in diameter and reaching 0.7 mm. in length produced on pinnule midribs and synangial pedicels. Spores spherical, 15 μ in diameter with crescent-shaped mark on exines.

Age: McLeansboro Group, Upper Pennsylvanian.
Locality: Berryville, Illinois.
Holotype slides: Slides 2996–3005 (from WCB 1239).

Summary

Two new species of *Scolecopteris* are recorded both of which were found in the Upper Pennsylvanian of Illinois. *S. monothrix* is distinguished by its long sporangia each of which has a distally attached long, multicellular hair. The tips of the component sporangia were tightly appressed when immature. The spores are very small and their number per sporangium high. *S. illinoensis* is characterized by having five or six sporangia per synangium, small spores, and conspicuous multicellular hairs on the underside of rachis and pinnules.

Acknowledgment

This study was carried out in the laboratories of Washington University under the guidance of Dr. Henry N. Andrews, to whom the writer wishes to express his sincere thanks; it is a part of a paleobotanical research program aided largely by the National Science Foundation. Thanks are also extended to Dr. Tom L. Phillips for assistance with paleobotanical techniques and for aid in other ways.

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EXPLANATION OF PLATE

PLATE V.

Scolecopteris monothrix

Fig. 1. Transverse section of a synangium sectioned in the plane 1–1 of fig. 4. Note spores passing into synangial cavity. Slide 2994. × 85.

Fig. 2. Transverse section of apex of synangium sectioned in the plane 2–2 of fig. 4. Note that all four apices fit closely together. Also note the four celled base of a sporangial hair (arrow). Transverse section of several hairs from other sporangia may be seen. Slide 2994. × 85.

Fig. 3. Longitudinal section of sporangial apex showing hair. "Bulb" at distal end is the point at which the hair leaves the plane of the peel. Slide 2988. × 100.

Fig. 4. Longitudinal sections of synangium and synangial hair indicating characteristic form and pedicellate attachment to the pinnule. Three separate sections from slides 2988, 2989, and 2990. × 50.

Fig. 5. Spores. Slide 2987. × 2250.

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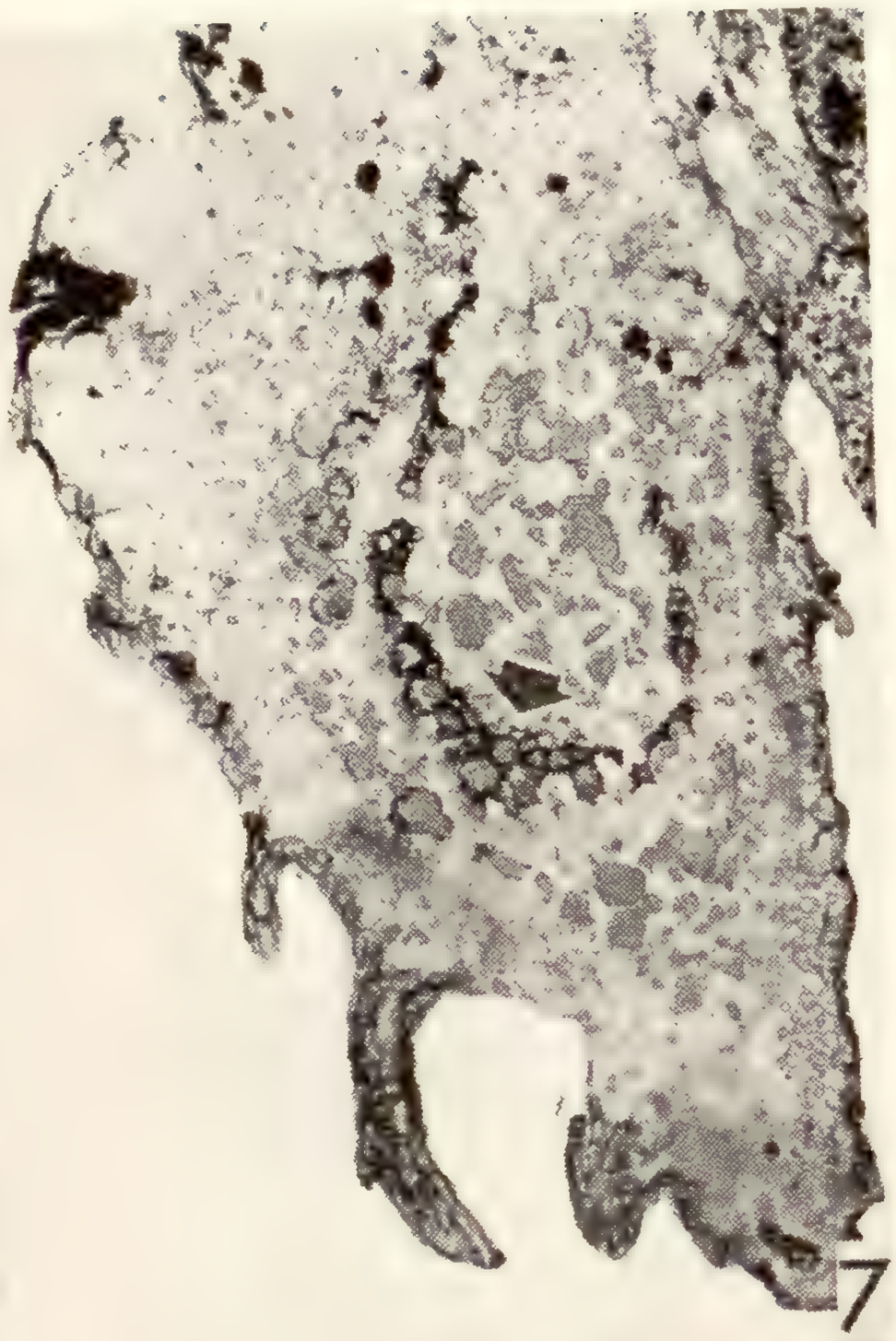
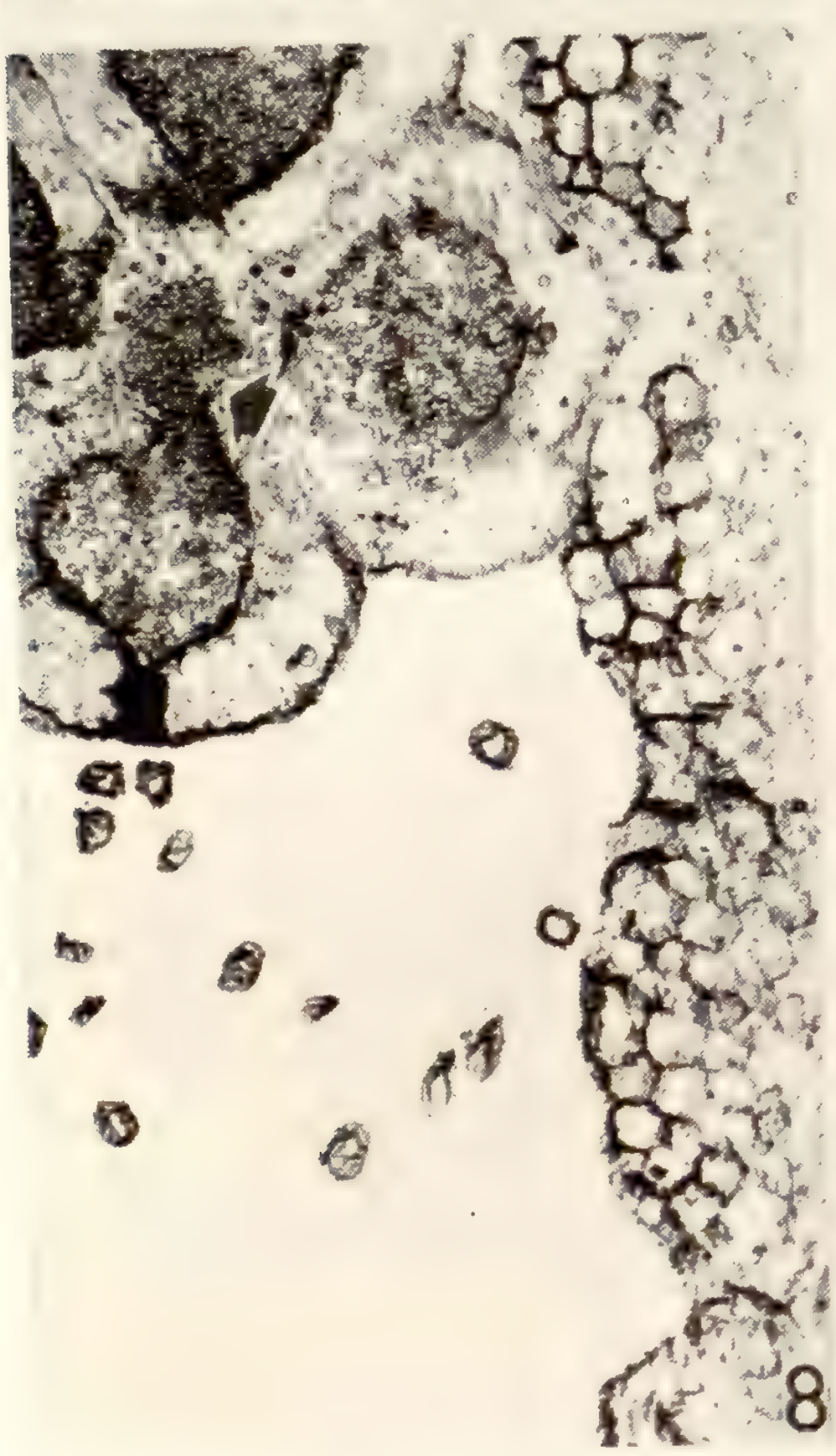
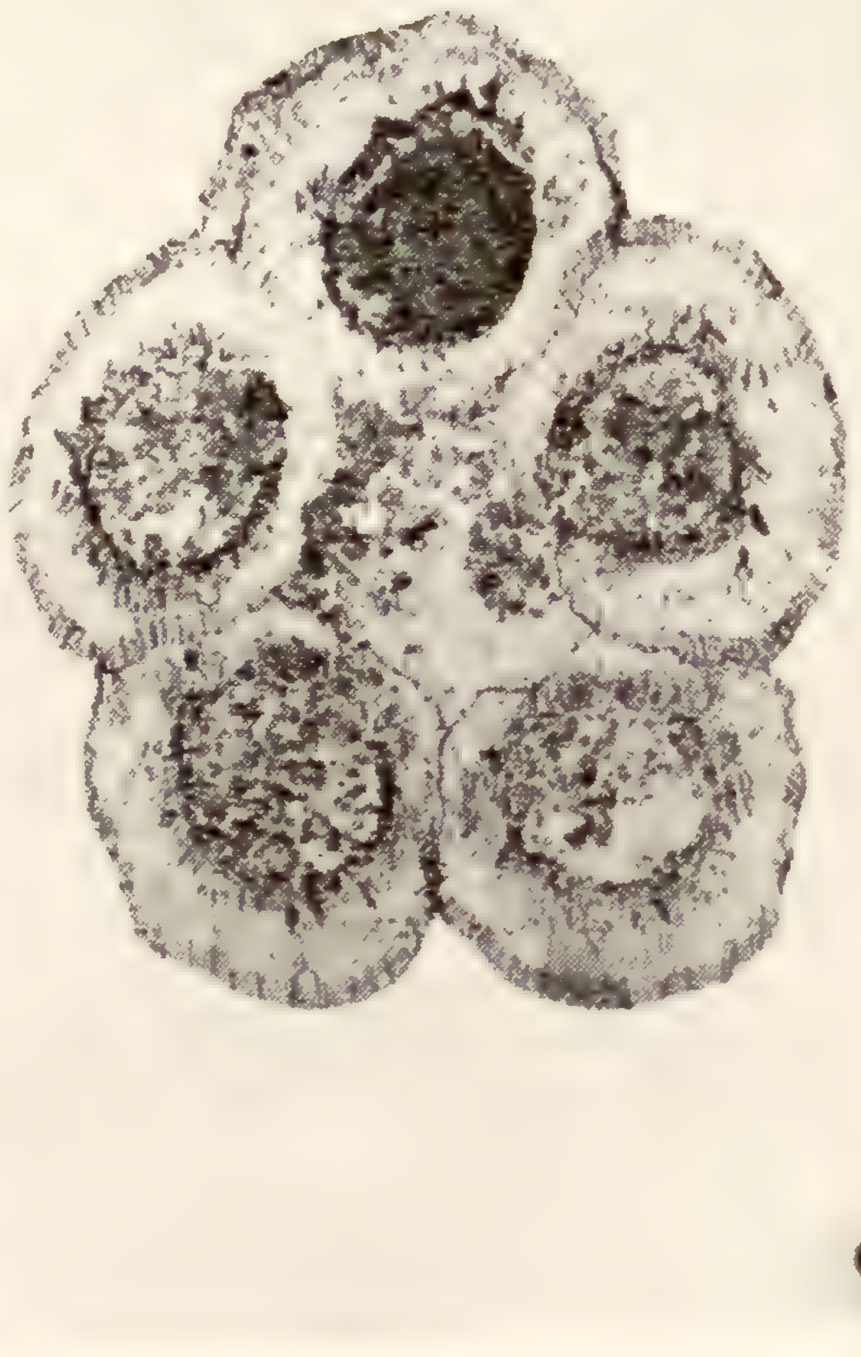






EWART—TWO NEW MEMBERS OF SCOLECOPTERIS

Explanation of Plate

PLATE VI.

Scolecopteris monothrix

Fig. 6. Longitudinal section of open synangium of more mature specimen. Slide 2992. × 50.

Fig. 7. Transverse section through midrib of rachis. Note U-shaped vascular strand (arrow) and hairs. Slide 2989. × 55.

Fig. 8. Transverse section through synangium, sporangial hairs, and inflexed pinnule margin. Note spore mass passing into synangial cavity (arrow). Slide 2994. × 85.

Fig. 9. Transverse section of a synangium consisting of five sporangia. Slide 2994. × 85.

Explanation of Plate

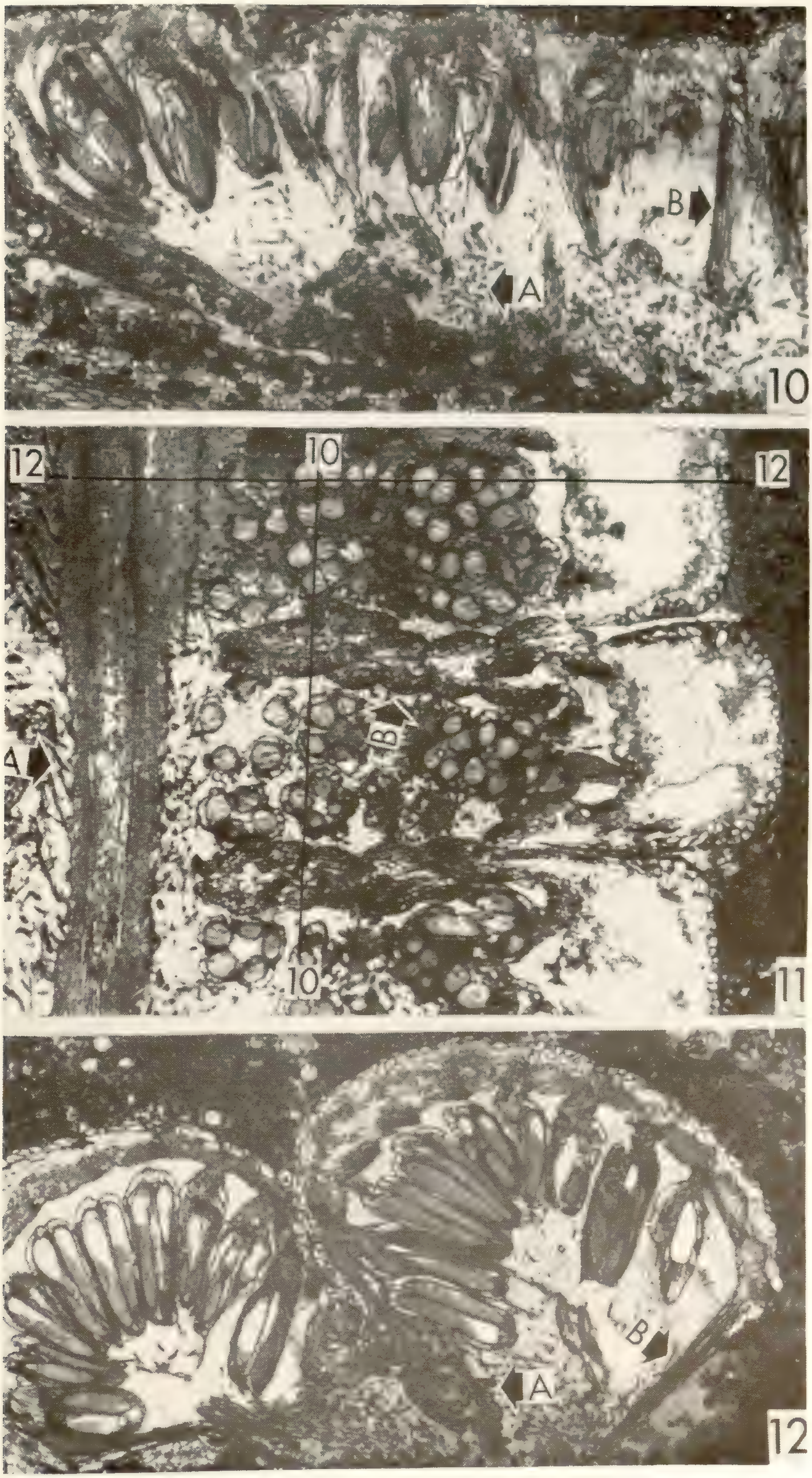
PLATE VII.

Scolecopteris monothrix

Fig. 10. Transverse section of pinnules in plane 10–10 of fig. 11. Note sporangial hairs (A) filling space below synangia. Slide 2995. × 13.

Fig. 11. Section of pinnules in plane of lamina. Note hairs on rachis midrib (A) and transverse section of pinnule margins (B). Slide 2993. × 15.

Fig. 12. Section at right angle to rachis midrib in plane 12–12 of fig. 11. Note rachis midrib (A) and strongly inflexed pinnule margin (B). Slide 2991. × 12.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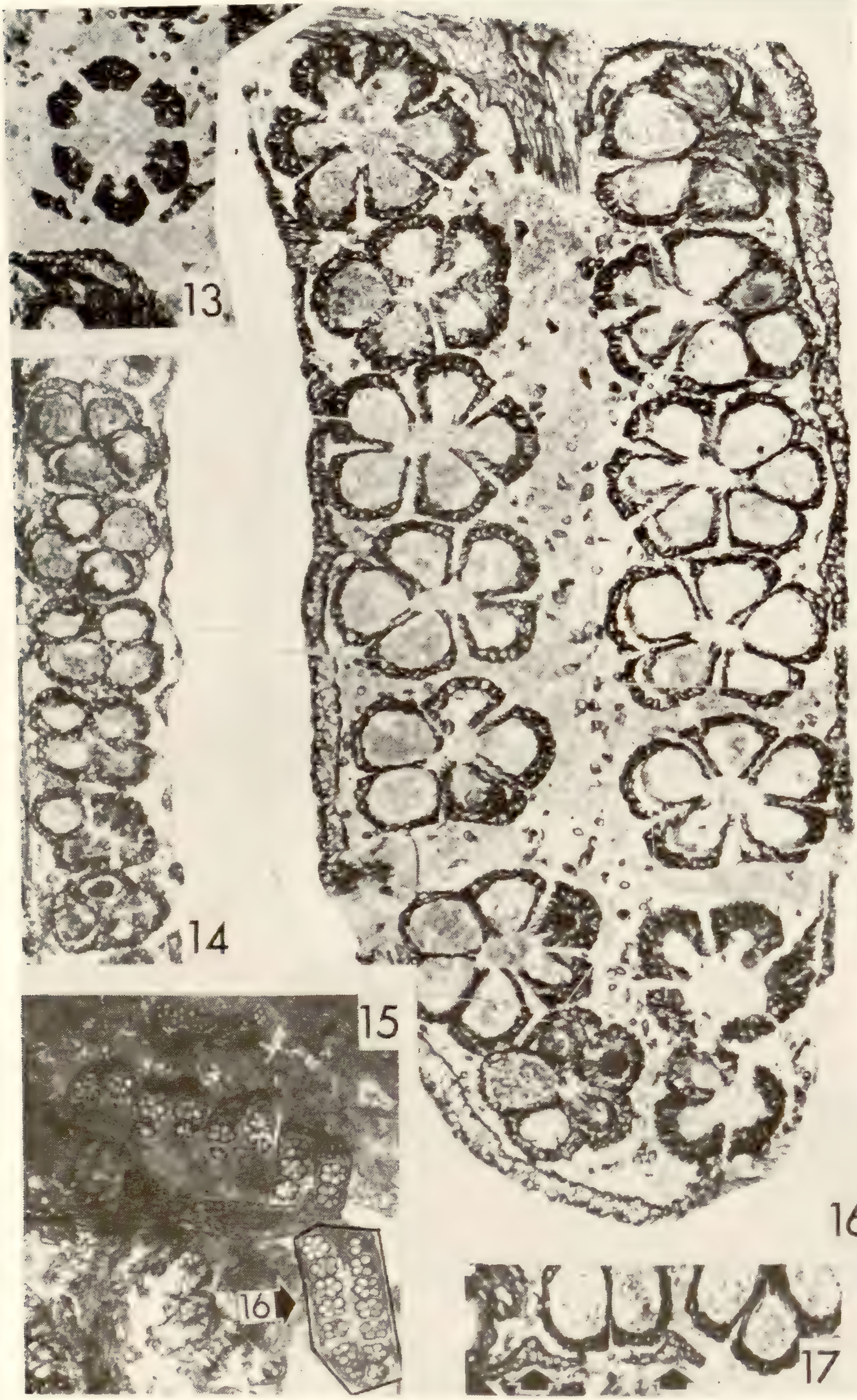


EWART—TWO NEW MEMBERS OF SCOLECOPTERIS

Explanation of Plate

PLATE VIII.

Figs. 13, 15–17. *Scolecopteris illinoensis*
Fig. 14. *S. minor* Hoskins

Fig. 13. Transverse section of a synangium in the region near the apex. Slide 3004. × 35.

Fig. 14. Transverse section of a row of synangia. Compare with *S. illinoensis* in fig. 16. Slide 3004. × 30.

Fig. 15. Longitudinal section of rachis midrib with attached fertile pinnules. Slide 3005. × 5.

Fig. 16 Single pinnule from fig. 15 enlarged. Note hairs in transverse section between rows of synangia. Slide 3004. × 35.

Fig. 17. Section through pinnule margin showing toothed nature of the margin (arrows). Slide 2998. × 35.

Explanation of Plate

PLATE IX.

Scolecopteris illinoensis

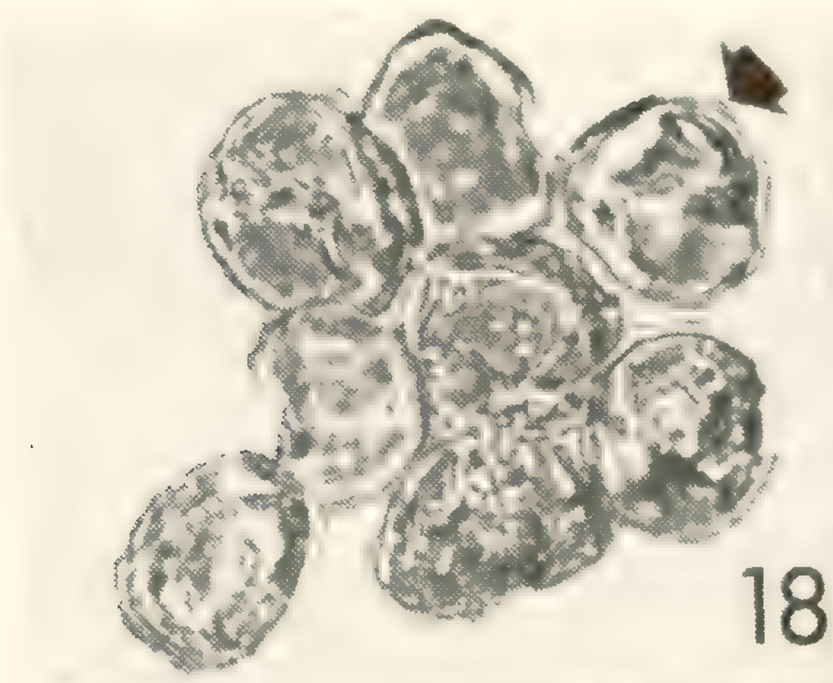
Fig. 18. Spores. Note crescent-shaped mark on exine. Slide 2996. × 1033.

Fig. 19. Obliquely transverse section of fertile pinnules. Note rachis midrib at extreme left. Slide 3003. × 6.

Fig. 20. Transverse section of half of a pinnule showing anatomical detail. A. Hypodermal cells (upper epidermis is poorly preserved); B. Palisade parenchyma; C. Spongy parenchyma; D. Lower epidermis; E. Pinnule midrib. Slide 3000. × 62.

Fig. 21. Transverse section of a fertile pinnule. Note long hairs on midrib. Slide 3001. × 57.

Fig. 22. Transverse section of a fertile pinnule. Note hair on sporangium and sporangium with spore mass. Slide 3001. × 57.



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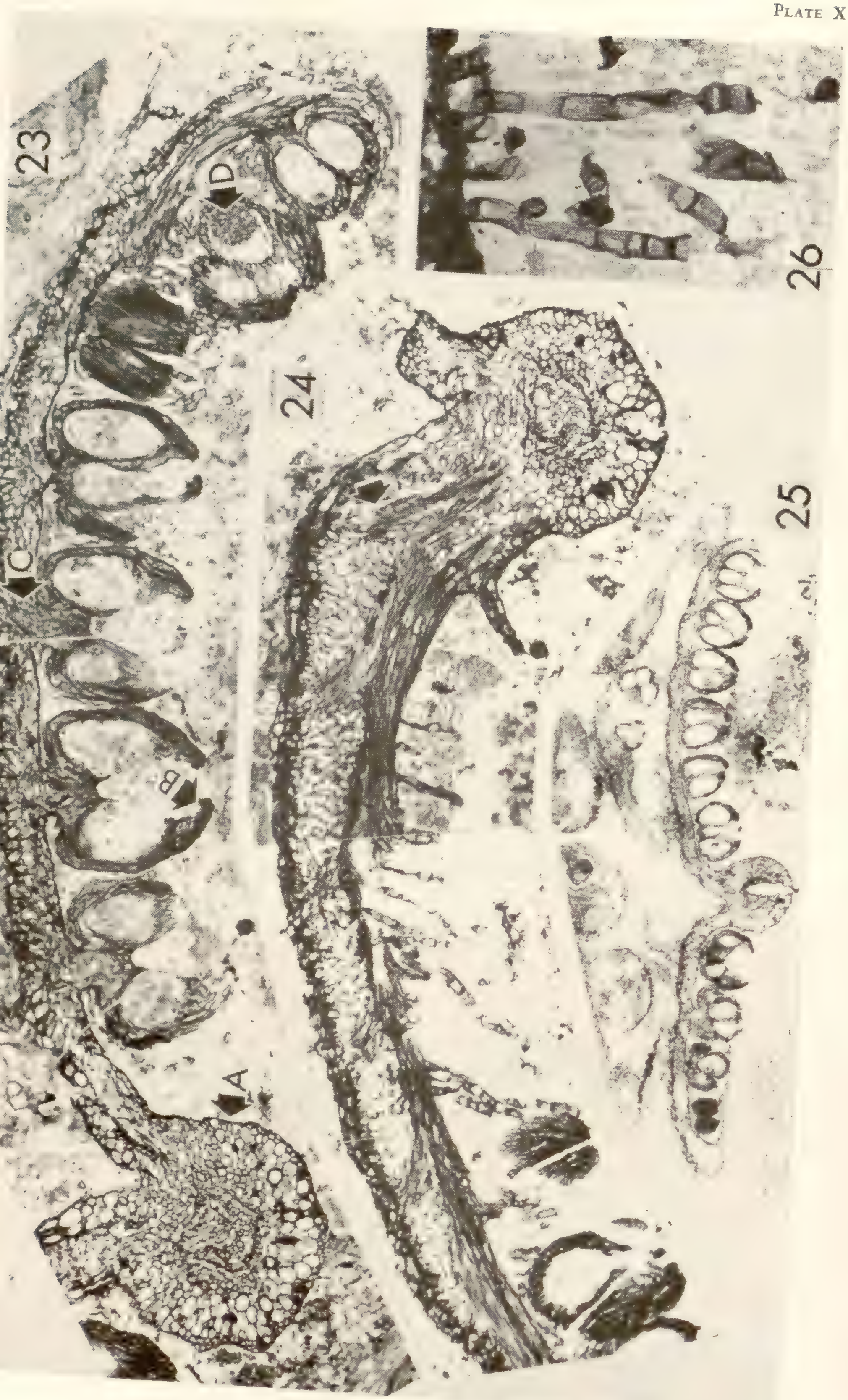
EWART—TWO NEW MEMBERS OF SCOLECOPTERIS

PLATE X



EWART—TWO NEW MEMBERS OF SCOLECOPTERIS

Explanation of Plate

PLATE X.

Scolecopteris illinoensis

Fig. 23. Longitudinal section of fertile part of pinnule. A. Transverse section of pinna midrib. B. Incurved apex of sporangium. C. Vascular bundle at base of synangial pedicel. D. Spore mass in sporangium. Slide 2997. × 33.

Fig. 24. Longitudinal section of pinnule midrib. Note vascular strands branching from midrib and hairs on midrib. Slide 2997. × 33.

Fig. 25. Section showing pinna midrib with pinnules on either side. Slide 3003. × 11.

Fig. 26. Hairs on pinnule midrib. Slide 2999. × 90.

PORTRAITS OF PLANTS. A LIMITED STUDY OF THE "ICONES"[1, 2]

ERNA RICE EISENDRATH

Abstract

A set of four criteria for defining the word "icones" is established: that the illustrations be full page in size; that they include some portrayal of the habit of growth of the plant; that they be botanically accurate; that they give aesthetic satisfaction. Each of the "icones" must fulfill each requirement in some degree, except in the plant portrayals of the 16th and 17th century herbals. The history of these cuts is traced throughout their oft-repeated use, and their exception to the general rule discussed in the light of their great botanical importance.

Four genera of the Cucurbitaceae *(Fevillea, Cucurbita, Lagenaria, Luffa)* are chosen as limiting factors in the study, and illustrations of these plants available in the library of the Missouri Botanical Garden discussed in relation to the criteria previously set up. The study is concluded with a chronological index of "icones" of these key species. Erna Rice Eisendrath, Henry Shaw School of Botany, Washington University, St. Louis 30, Missouri.

Botanical Use of the Word "Icones"

The word "icones" was taken into botanical parlance by Otto Brunfels in 1530. Its spelling in the title of his *Herbarum vivae eicones* still conveys a hint of orientalism just strong enough to tie in with its common meaning today; to the layman, an icon is (as it was, to the publishers of Webster's *New International Dictionary* of 1918) "a religious image in the Eastern church". For botanists, however, it is not the gilt on these distorted saints that glows when they speak reverently of "icones". Their enthusiasm is evoked by a kind of floral illustration which they automatically lump as "icones" in special sections of libraries; to which they readily refer as "icones" in conversation; of which they will confidently name names as true "icones"; but for which they hesitate to pronounce a definition. So, though everybody knows the special meaning of the word, there remains the problem of establishing criteria by which to implement its definition; a later problem will be to list the books containing illustrations that satisfy the criteria.

To start from an authoritative beginning I give you Benjamin Daydon Jackson, who in 1900 first published in London his most useful *Glossary of Botanic Terms.* To him, "icones"[3] are merely "pictorial representations of plants; botanic figures". In this sense which includes all botanical illustrations it was certainly used by Pritzel[4] in his *Iconum Botanicarum* of 1855 and is also so used in the Latin title page of the *Index Londinensis.*

For the purposes of this paper, however, I prefer basing my criteria on the last word of the last definition of "icon" given in the *Oxford English Dictionary* (Oxford, 1933): "esp. applied to 'figures' of animals, plants, etc. in books of Natural History. Obs." The use of "icon" to include all natural history illustrations is now obsolete; when botanists speak today of the "icones" it is with a

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[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Master of Arts.

[2] The author wishes to express her gratitude for their help in preparing this manuscript to Dr. Edgar Anderson, Dr. Hugh Cutler and Dr. George Van Schaack.

[3] Jackson's definition is given for the plural form more commonly used by botanists than the singular.

[4] "The task which Pritzel set himself in the preparation of his Index was to record in the simplest way all 'valuable' figures of Phanerogams and Ferns, excluding, with certain exceptions, those of the pre-Linnean period." (O. Stapf, Hon. Editor of the *Index Londinensis*, in Introduction to the 1929 edition.)

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different connotation, not specifically stated in any source that I can find. It implies more than scientifically accurate illustrations, and more than attractive plant portrayal, falling some place between the two and partaking of both but, with a kind of hybrid vigor, better than either. Dr. Hugh Cutler bravely ventured to make the following brief but telling statement. "The 'icones'," he said, "may have nothing to do with the church exactly, but a great many botanists worship them." That is, apparently, about as far as educated angels dare to tread; this fool will now step in to define "icones" by establishing the criteria which distinguish them from other illustrations in botanical books.

Criteria Distinguishing "Icones"

After examining every lead to illustrations of the key[5] genera of Cucurbitaceae available at the Missouri Botanical Garden library (some 157 volumes), I have set up four arbitrary criteria for "icones". The first is that the illustrations be full page[6] in size; the second, that they include portrayal of the habit of growth of the plant. The third is botanical accuracy, and the fourth artistic presentation.

In many instances my first criterion is necessitated in order to eliminate illustrations used simply as elaborations of a text. According to Nissen (1951), "the documental botanical illustration should, for the co-investigator, replace the plant itself, be he distant in time or place".[7] So, too, must true "icones" be visual portraits of plants, dependent in no sense upon the written word. P. J. F. Turpin, the great French botanical artist, quite naturally believed that the brush was greater than the pen as a naturalist's tool, and wrote that he "who possesses only the latter loses perhaps the more significant" (Turpin, 1820). But the brush used to depict the plant must do so in considerable detail, and the portrait must be extremely accurate—so accurate as to compete with the botanist's dried herbarium specimen as a source material for study. (The possibility of this is recognized in the official acceptance, though rare, of such representations as type specimens.) Small figures of plants cannot possibly fulfill all of these requirements; hence the first criterion for true "icones": that they be full page illustrations.

My second criterion for defining true "icones" is that they represent the habit of plants, and include both vegetative and reproductive organs. It is possible to object that this is unnecessary, since one can assume that generic characters are "given", and that only identifying specific characters need be depicted in plant portraiture. This objection I liken to a statement that a man's fingerprints identify him; certainly they will differentiate him from all other men, as certain characters of a species of plants will also differentiate it. Neither fingerprints nor selected characters, however, will give us portraits of the individual or the species, and, in defining today's usage of the word "icones", I insist that portrait is the proper synonym (if any is truly proper).

"Icones", then, must portray habit of growth, and here is another example of the need to pin a word to exact definition. What is "habit"? Webster (*New*

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[5] See p. 296.

[6] For many 16th and 17th century herbals this criterion must be ignored for reasons explained later in the text.

[7] Translated by Mr. Alfred Sadler.

Intern. Dict., 1918) gives as its eighth definition of the word, "*Nat. Hist.* Characteristic form or mode of occurrence or growth; as, elms have a spreading *habit*." Jackson, deriving "habit" from the Latin, gives, "The general appearance of a plant, whether erect, prostrate, climbing, etc." Sir Joseph Dalton Hooker, the great systematist, Director of Kew Gardens, and editor of volumes 91–130 of Curtis' *Botanical Magazine*, wrote, "Habit of a plant, of a species, a genus, etc., consists of such general characters as strike the eye at first sight, such as size, colour, ramification, arrangement of the leaves, inflorescence, etc., and are chiefly derived from the organs of vegetation" (Hooker, 1875–97). To this I append the requirement that either flower or fruit must be depicted; however, it is not always easy to decide where "habit" is illustrated and where it is not.

I have, for instance, not listed among the "icones" pertinent plates (see plate XI) in Tournefort's *Institutiones rei herbariae* (1700), even though they are cited by Linnaeus (*Species Plantarum*, Stockholm, 1753, vol. 2, pp. 1010–1011) in his original description of the genus *Cucurbita*. My reasons are that Aubriet illustrated for Tournefort only parts of plants—fruits (and with dissections, too!), seeds, flowers, peduncles, etc., but no idea of the appearance of the plant itself is given. Again, L. H. Bailey, in his *Garden of Gourds* (1937), includes page after page of drawings, almost all of which show sections of the stem, flowers, fruits and leaves. Since they also show tendrils where tendrils exist, it is apparent that such plants would climb if given a chance to do so, and I have therefore listed a number of these illustrations among the "icones"; but I have eliminated such as that of the "Mock Orange" variety of *Cucurbita Pepo*, which depicts a pistillate flower, a fruit with peduncle attached, a tendril, a stem in cross-section, and enlarged dissections of the style and stigma, as well as of the anther column; but habit, no!—so it is not listed.

In this connection it is interesting to note that only the earliest "icones" illustrate the root. This is undoubtedly a loss to plant portrayal, and probably came about when interest in plants shifted to a taxonomic basis from the pragmatic approach of the rhizotomists and their followers. These predecessors of the herbalists performed magic and cures based on lore often dating from the Greek period, and generally associated, in popular folk ritual, with properties inherent in plant roots (Singer, 1928). Also worth noting is the rarity of portrayal of habitat along with habit. This is so important a factor in the systematics of botany, and was used so wonderfully by Audubon in his portrayals of birds and animals, that one wishes it were more often used as backdrop to "icones" of our flora. Nissen's (1951) statement, "Plant sociology . . . is of recent date, and representation of it is prepared more and more with the camera,"[8] very possibly explains this lack.

If the portrait of a plant belongs at all within the field of botany, it must be scientifically accurate, my third criterion for "icones". The degree of precise detail will vary in each plant portrait, as it does in human portraiture. There is, however, a most important difference in the requirements of the two. A portrait of a man shows all the artist can tell us about a single individual, be he godlike or sickly earthling; but, to quote from Arber (1938), "the drawing which is ideal from the standpoint of systematic botany, avoids the accidental peculiarities of any indi-

[8] Translated by Mr. Alfred Sadler.

vidual specimen, seeking rather to portray the characters fully typical for the species." This distinction is well illustrated in the very book that introduced the word we are trying to define, Brunfels' *Herbarum vivae eicones*: here we find that some of Weiditz' magnificent "living portraits" exhibit such "accidental peculiarities", probably as a result of an overly enthusiastic return to direct observation from nature. Note figure 1, of Weiditz' *Arctium lappa L.*, in which the plant's poor wilted leaves add nothing except the information that it had been pulled from the earth too long before Weiditz got around to drawing it. He apparently did not itch, as Tournefort felt the true botanical artist should, to get his observations on to paper. "It frets a man", Tournefort wrote (quoted from Blunt, 1951) "to see fine Objects and not be able to take Draughts of them; for without this help of Drawing, 'tis impossible any account thereof would be perfectly intelligible." The requirements of accurate botanical illustration are that the characters of a species be accurately represented; fortuitous accident in the life story of the individual, such as its being attacked by voracious insects, is of no interest to anything or anybody but the insect and the plant.

It is almost pedantic to add that accuracy is not impaired by the additional quality of aesthetic satisfaction, the fourth of my criteria. Among the "icones" the two are found in variable proportions, the balance being struck not only on the basis of the purpose for which the pictures were made, but also depending upon the date of their publication. The demands of fashion in taste and interest can be followed clearly throughout the centuries. Many flower illustrations of great decorative quality have no botanical value whatsoever, and quite correctly end their usefulness as lamp shades; this kind of work reached its nadir in the 19th century, when spinster ladies sentimentally painted charming bouquets on china, as well as any other available surface. When these illustrations appeared in books, they were usually accompanied by saccharine verse, under such titles as *The Moral of Flowers* (Marquand, 1947).[9] Today's floral illustrations represent the opposite extreme. We tend to file scientific data in compartments well isolated from all aesthetic consideration; for this reason we must beware of eyeing with suspicion the accuracy of figures that are pleasing. It is important to remember, as is subsequently discussed, that the "icones" include the work of Turpin, Fitch and many other extremely gifted artists, whose talents were exhibited in a field that demanded far more of them than simple art for art's sake.

An aesthetic quality, then, is the last of four criteria set up for true "icones"; full page illustration, portrayal of habit and botanical accuracy have all been discussed above. Extremely few illustrations will pass all these tests; but who

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[9] The sentimental (or should I say romantic?) approach cannot be limited entirely, however, to spinster ladies or to the 19th century. Linnaeus himself effused most colorfully: "The petals of the flower contribute nothing to generation but serve only as bridal beds, gloriously arranged by the great Creator, who has adorned them with such noble bed-curtains and perfumed them with so many sweet perfumes that the bridegroom may celebrate his nuptials with all the greater solemnity. When the bed is thus prepared, it is time for the bridegroom to embrace his beloved bride and surrender his gifts to her." And Erasmus Darwin, grandfather of Charles, versified,

"With honey'd lips enamoured woodbines meet,
Clasp with fond arms, and mix their kisses sweet."

(Both quotes are from Krutch, Joseph Wood, *The Gardener's World*, New York, 1959; p. 24.)

Figure 1. "De lappis" *(Arctium lappa)*, vol. II. p. 62, *Herbarum vivae eicones*, Otto von Brunfels, Argentoreti, 1531.

knows better than a botanist that taxa must be elastic, and that no set of characters is invariably true for all the units that the taxon must include!

"Icones" may be found in regional floras, de luxe tomes concerned only with the plants growing in a single garden, learned treatises on classification, serials published by scientific institutions or nurserymen's catalogues. All of these fall within the enormous body of illustrated botanical literature, of which the *Index Londinensis* lists well over 3000 titles, and for the purposes of this paper it was necessary to establish a limited approach. One could set up chronological barriers, choosing, as did Sitwell and Blunt (1956), two centuries as a high point in botanical illustration. One could profitably discuss only the work of one great artist, such as Turpin, whose name appears several times on these pages. One could trace any of several aspects of the subject through the pages of Curtis' *Botanical Magazine* during its almost two hundred years of publication. Or, one can approach this loose aggregate of illustrated books with a particular subject as the tool by which to cut it down to workable proportions. This method has been used, with four genera of the Cucurbitaceae the limiting factor.

Key Species of the Cucurbitaceae as Limiting Factors in This Study

Various reasons may be cited for pursuing the study of "icones" through illustrations of members of the Cucurbitaceae. As is later discussed, the family is generally distinguished by a fleshy fruit, a structure known as a "pepo"; but, whereas in many plant groups the fruits may be used to delimit various taxa, it cannot be said of the cucurbits that "by their fruits ye shall know them". There are "pepos" and "pepos", and the close relatives, among many cultivated forms, will produce offspring which exhibit tremendous differences. In size alone, the "pepo" may be as small, let us say, as a tangerine, or absolutely enormous, as witness the Hubbard squash or the long-as-a-man-is-tall *Lagenaria.* It is never possible conveniently to mount (and seldom even to preserve) such fruits as herbarium material; therefore, since it is for the edible, decorative and useable fruits that the family is cultivated, illustrations of them are of great botanical importance.

The flowers, too, present a problem in survival. Though they may be showy, they collapse dismally after one day of glory in the sun, a sad truism for the taxonomist, since they present most interesting morphological variations. (It may be due to the same truism that the work of many of the best known floral artists does not appear among "icones" of the Cucurbitaceae; an illustrator who attempts to draw them painstakingly from life will find that their lives are too brief to enable him to create the illusion of prolonging them!) The choice of the key genera was made for several reasons: *Fevillea* because it is the primitive group in the family, serving as starting point for a number of phylogenetic series; *Cucurbita, Lagenaria* and *Luffa* because their distribution is so wide and varied as to insure their appearance in a variety of publications.

The Cucurbitaceae include about one hundred genera (fide Lawrence, 1951). Not only the placement of the family in a natural system, but also the delimitation of generic characters have intrigued and baffled botanists over the years. This problem is, however, entirely beyond the scope of my study.

The Cucurbitaceae are generally tropical plants, with some species hardy enough to extend into the temperate zones. All, however, are frost-tender herbs, and survive to fruit in chilly climates only because they grow very rapidly. *Cucurbita* is native to the American tropics, and *Luffa* (with the exception of *L. operculata,* also New World) to the Old World tropics, whence *Lagenaria* probably also came, but this genus has been for a very long time universally distributed throughout the warm parts of the world.

The same three genera are of interestingly varied economic importance. *Cucurbita* is cultivated for its edible and decorative fruits, the pumpkins and squashes which traditionally are staples of the American diet, and archeologically are known to have been important long before the advent of the white man to either American continent. *Luffa's* fruit has a fibrous interior when mature which, dried, becomes the "vegetable sponge" so widely used by masseurs; the young fruits (apparently less abrasive!) are edible. *Lagenaria* fruits in an incredible variety of forms; wherever it is grown, it teases the imagination to put the fruits to use as ladles, vases, pitchers, bird houses or merely decorations. A visitor to Georgia and Florida at the turn of the century (Odell, 1904–05) found that "hardly a domestic operation there is complete without the aid of the Gourd in some form". It was even used as a cradle for negro babies!

Fevillea (tropical American) is neither widespread nor economic, but is included because it is not cultivated, which fact, along with its many primitive characters, presents interesting botanical contrasts to the other genera. In *Fevillea,* for instance, the corolla is distinctly polypetalous, as it is also in *Lagenaria.* In *Luffa* it is deeply lobed; in *Cucurbita* the five petals are joined in a floral tube. Again, in *Fevillea* five stamens with biloculate anthers of an unspecialized type stand perfectly free, alternating in position with the petals; in *Luffa,* as in the other three genera, there are usually basically only three stamens (because of the coherence by their filaments of two pairs of the original five), but they are borne free on the calyx tube. In *Lagenaria* the anthers of the stamens cohere lightly, but are not truly connate; in *Cucurbita* the filaments are connate (except that sometimes they are free at the very base) and the anthers are twisted so inextricably together in a column as to be almost indistinguishable. In none of the last three genera are the anthers primitively biloculate; they dehisce by a single longitudinal split.

Of the books listed below, the following contain "icones" of *Fevillea*: Marcgrave-Piso, Plumier, *The Botanical Magazine, Dictionnaire des Sciences Naturelles,* Descourtilz, Martius, Velloso, Engler and Rendle. Of these, all but the serial, the dictionary and the systematists concern plants of the Caribbean and South America, the earliest of them being Marcgrave's first edition in 1648.

Lagenaria is illustrated, among the books listed below, by Fuchs, Dodoens, L'Obel, Dalechamps, Tabernaemontanus, Gerarde, Parkinson, Bauhin, Rheede, Rumpf, Oskamp-Zorn, Descourtilz, Velloso, Iinuma, Duthie and Fuller, Bettfreund and Bailey, indicating an early European knowledge of the plant, as well as its wide spread in tropical areas of the world.

Luffa, rather strangely, is not pictured by those earlier herbalists who illustrated

Lagenaria, though both genera are thought to have originated in the Old World tropics. Among the "icones" listed we find *Luffa* first in Vesling, illustrating Egyptian plants in 1638. It appears next in Commelin, illustrating the plants cultivated in the Physic Garden of Amsterdam in 1706; later, it is pictured by Rheede, Rumpf, Cavanilles, *The Botanical Magazine*, Velloso, Martius, Wight, Iinuma, Blanco, Duthie and Fuller, Lecomte, Engler and Bailey. This indicates a wide distribution indeed, although the plant was apparently not cultivated in Europe as early as was *Lagenaria*.

Of the four genera considered in this study, *Cucurbita* is not only the best known and most widely cultivated today, but archeologically it is of great interest, being found in diggings where it can be used to trace the agriculture of early man in the so-called New World. Because of its tremendously variable fruits, seeds and other organs, *Cucurbita* also challenges the systematist and intrigues the geneticist; because its floral parts are large, it is useful to morphologists and physiologists and, because the cucurbits are easily grown, their large fruits can be retained for study, while their indeterminate growth permits flowering from maturity to frost. As a matter of fact, *Cucurbita* presents satisfying study material for most botanical specialists, though geneticists, pleased with the large pollen mother-cells, find difficulties in their miniscule chromosomes (Whitaker and Bohn, 1950). However, it is probably because of its edible and decorative fruits that we find among the "icones" more illustrations of *Cucurbita* than of the other three genera selected.

The earliest "icones" of *Cucurbita*, the two appearing in the fabulous folio edition of Fuchs, 1542, are probably also the most beautiful. We find *Cucurbita* next in the 1552 Aztec herbal known as the *Badianus Manuscript*; and at short intervals from then on, mostly in pictures derived more or less from Fuchs, cucurbits appear in Matthiolus, Dodoens, L'Obel, Dalechamps, Tabernaemontanus, Gerarde, Parkinson and Bauhin. Original figures are found in Rheede, Rumpf, Buch'oz, Schkuhr, Vietz, Descourtilz, Chaumeton, Wright, Iinuma, Blanco, Duthie and Fuller, Bettfreund and Bailey. The list evidences a rapid and wide spread of knowledge about and interest in the plants.

Earliest Illustrations of Key Species

None of the titles in the list of "icones" of the selected genera predates 1542, the year of publication of Fuchs' *De historia stirpium*. This fact is significant because the historical background to a discussion of plant illustration is strangely poor. Though all of man's existence (along with that of other animals!) must of necessity have been ultimately dependent upon the flora of his world, relatively very few early examples of plant delineation are known, in comparison to those of fauna. Among the key genera, the earliest I find are chance reprints in modern books, all of *Lagenaria*. The first is printed by Behling (1957), and is taken from the manuscript *Tacuinum Sanitatis* in the Austrian National Library. It is described as a page from the

> "Hausbuch der Cerutti, of upper-Italian origin, from the turn of the 14th to the 15th century. . . . One sees the flask-shaped gourd (*Cucurbita lagenaria*, L.) in an excellent example, hanging in a thicket of leaves. The text below declares . . . that the gourd is cold and moist . . . and most useful to be eaten fresh and green. It stops thirst."

The second reproduction is Arber's plate iii (1938). This is from Konrad von Megenberg's *Das Puch der Natur*, Augsburg, 1475, which contains the first printed plant illustrations. It shows, in the center of a group of plants, an unmistakeable *Lagenaria* fruit, pendulous on a terminal branch, the whole plant arising from a basal rosette of heart-shaped leaves. The third is in a 1940 facsimile of an Aztec herbal of 1552 (Codex Barberini, Latin 241, in the Vatican Library). Familiarly known, from the name of its translator, as the *Badianus Manuscript*, it was put together by Martin de la Cruz, described in the text as an "Indian physician . . . who is not theoretically learned, but is taught only by experience" (Arber, 1938). The colored illustration shows a *Cucurbita foetidissima*, so identified as the leaves and root seem to belong to a perennial plant. In the herbal it is called the "Ayonel-huatl", translated as "calabash root", and is described as an ingredient of a complex concoction recommended to relieve the pain of childbirth.

Fuchs' De historia stirpium

Fuchs' beautiful *De historia stirpium* was published in Basle in 1542, twelve years after Brunfels introduced "icones" as a botanical word. Like Brunfels', Fuchs' book is illustrated with portraits of plants made by artists who had actually looked at them. This statement does not seem startling, but it has great significance. Plant illustration in the herbals, prior to Brunfels and Fuchs, consisted of constantly recopied figures, derived from ancient originals, which in each reproduction lost more of their freshness and validity. Strangely, the invention (circa 1450) of movable-type printing, with its tremendous impact on the dissemination of all kinds of knowledge, did not immediately influence publishers to have their artists take a fresh look at plants. And this, despite the fact that illuminated manuscripts of the period often include charmingly naturalistic flower paintings, and that such artists as the Van Eycks, Van der Goes, Jacopo Bellini and Botticelli painted flowers beautifully even before a magnificent high of superb flower portrayal was reached in the work of Leonardo[10] (1452–1519) and Dürer (1471–1528).

Brunfels and Fuchs let fresh air into the musty chambers of illustration of the herbals, Fuchs leaving for us fine woodcuts of both *Cucurbita* and *Lagenaria*; but it is from them (see below) that subsequent generations of herbalists were satisfied to derive their illustrations, thus slamming down the window once again.

Fuchs shared with Brunfels the realization of the importance of drawing plants from life, but his artists, unlike Weiditz, (whose "living portraits", you will remember, were sometimes limited portrayals of individual plants) also understood the necessity of depicting plants typical of a species. From his own statement we know that Fuchs worked closely with the artists.

> "Each (picture) . . . ", he wrote in his preface, "is positively delineated according to the features and likeness of the living plants; we have taken peculiar care that they should be most perfect, and, moreover, we have devoted the greatest diligence to secure that every plant should be depicted with its own roots, stalks, leaves, flowers, seeds and fruits. Furthermore we have purposely and deliberately avoided the obliteration of the natural form of the plants by

[10] Leonardo wrote, "The painter will produce pictures of little merit if he takes the work of others as his standard; but if he will apply himself to learn from the objects of nature he will produce good results." (Quoted from MacCurdy, Edward, *The Notebooks of Leonardo da Vinci*, New York, 1954; p. 902.)

shadows, and other less necessary things, by which the delineators sometimes try to win artistic glory." (Quoted from Arber, 1938.)

Fuchs was himself a physician, famed throughout Europe for his successful treatment of an epidemic disease that hit Germany in 1529, but his love of plants was more than a professional interest. Again in his preface, he wrote,

"There is no one who does not know that there is nothing in this Life pleasanter and more delightful than to wander over woods, mountains, plains, garlanded and adorned with flowerlets and plants of various sorts and most elegant to boot, and to gaze intently upon them. But it increases that pleasure and delight not a little, if there be added an acquaintance with the virtues and powers of these same plants." (Quoted from Arber, 1938.)

Fuchs' great work represents the high point of the Renaissance herbal (Singer, 1928); the text has the botanical limitations of all herbals, but the illustrations are superb. The figures, fitted gracefully into the frame of the full folio page, do not thereby lose their naturalism. The lack of shading that Fuchs mentions sometimes makes the outlines appear thin, but this is much relieved by the presence of color, which the artists probably intended should be applied by hand, after printing (Blunt, 1951).

The large folio plates of the key genera include two of *Cucurbita Pepo,* called by Fuchs "Cucumis Turcicus" and "Cucumer Marinus", and three of *Lagenaria vulgaris,* labeled respectively "Cucurbita Maior", "Cucurbita Minor" and "Cucurbita Oblonga".

In 1545 an octavo edition of Fuchs appeared which contained the same illustrations of the plants under discussion, with exactly the same names given them, but in very much reduced size and mirror images of the larger cuts.[11] They were to have a long life indeed.

These small-scale cuts from Fuchs, along with some from other sources, were used for over a hundred years by subsequent generations of herbalists. It would take a contortionist to squeeze these overused or derived plant illustrations into the criteria set up for "icones"; but I feel they must nonetheless be included in this study, and I claim justification from the excellent authority of Dr. William Trelease, first director of the Missouri Botanical Garden. Dr. Trelease wrote,

"No study of the cultivated plants of the present time can be at all complete unless the minute and painstaking records of the herbalists are consulted, for, with so mutable a class of plants as our flowers, vegetables, farm crops and fruits, the tracing of their history under cultivation is no small part of their study. What is asserted of cultivated plants . . . is also true, though to a less degree, of the native plants . . ." (Trelease, 1896).

We shall see that a number of the plant figures of the herbalists are far from "painstaking records", but we shall also see that others which my definition would carry me by with the merest swish of the skirt, play important roles in Linnaean classification.

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[11] Illustrations can be mechanically changed in size by use of a pantograph. This instrument, constructed of four bars, has a pencil placed at the juncture of two of them, another at the tip of a third. As a system of levers, the pantograph can be so adjusted that while one pencil traces a picture, the second reproduces it in the desired different scale. The new picture can then be pasted to an uncut block, traced thereon and a new cut made. As we shall see, the new cut often prints a mirror image of the original, because of the way the new picture is glued onto the block. (I am indebted for much of this information to Finan, John J., *Maize in the Great Herbals*, Ann. Missouri Bot. Gard., 1948; 35:8–186.)

With Fuchs' "icones" well in mind, we now embark upon an unbelievably complex task, tracing from his and other true portraits of plants the often inadequate thumb-nail sketches used and reused by successive herbalists.

Woodcuts Derived from One Source and Used by Several Authors

Bailey (1929) identified Fuchs' "Cucumis Turcicus" as "undoubtedly a *Cucurbita Pepo* of the vegetable marrow kind", and Whitaker (1947) agrees. In 1563, in his *Cruydeboeck,* Dodoens reproduced the smaller cut as "Pepones magni", using it again in 1616, in his *Stirpium historiae pemptades,* as "Pepo maior oblongus". In 1587, in his *Historia generalis plantarum,* Dalechamps, possibly using the same cut, called it "Cucurbita Indica longa", and in 1636 Gerarde, in *The herball,* described it as "Pepo maximus oblongus". The picture ends its career, as far as I know, as "Cucurbita foliis asperis sive Zucha, flore luteo, Ic. II" in Johannes Bauhin's *Historia plantarum* of 1650. This last derivative from a magnificent original has been cut down to diminutive measurements (8½ × 4½ cms.); the tendrils of the plant are so stylized as to be almost indistinguishable organs, the character of the peduncle at the point of attachment is entirely lost, and the illustration becomes as far removed as possible from a portrait of a living plant.

This series presents a good example, however, of the botanical significance of many of the small derived wood-cut figures of the herbals. Linnaeus in his definition of *Cucurbita* (*Species plantarum,* 1753, vol. II, p. 1010) cited a variety *β* with Caspar Bauhin's *Pinax* as reference. Caspar, the son of John, did not illustrate his book, but referred to the pictures mentioned above, from Dodoens' work of 1616 and Gerarde's 1636 *Herball,* so Linnaeus' description is indirectly descended from a picture which may be described as a foster child of Fuchs'.

Again, Fuchs' "Cucumer marinus" had a long and mostly unhappy history (see Figures 2, 3 and 4). Matthiolus (*Commentarii in libros sex Pedacii Dioscoridis de materia medica*) in 1558 printed as "Zucche Indiane" and in 1560 as "Cucurbita Indica" a plate which is certainly not a direct copy of Fuchs', but which almost as certainly was copied from his. Dalechamps in 1587 used Matthiolus' cut, in mirror image, as "Cucurbita Indica rotunda", and Linnaeus (*Species plantarum,* 1753, vol. II, p. 1010) cites Dalechamps as a reference for his *Cucurbita Pepo.* Bailey (1929) says of this cut that it represents

> "a tendril-bearing plant; and the fruit stems are long, apparently ridged and not enlarged next to the fruit; the leaf shape also answers well for the species we know as *Cucurbita Pepo.* The hairiness along the stem is undoubtedly exaggerated; and the leaf-bearing to the roots is conventionalized as well as the mode of fruiting."

In 1563 Dodoens printed a cut more exactly derived from Fuchs' octavo "Cucumer marinus", calling it "Pepones rotundi", and in 1616 Dodoens reused it, this time as "Pepo rotundus minor". By 1636, when Gerarde called it "Pepo minor sylvestris", the detail was considerably coarsened, but it is very possible that the same plate was used. In 1650 Bauhin printed another poor, small, derivative cut, this one "Cucurbita foliis asperis sive Zucha flore luteo, Ic. V."

Fuchs' illustrations of *Lagenaria,* too, produced a motly swarm of progeny. His "Cucurbita oblonga" is in Dodoens, 1563, as "Cucurbita anguina", and in Bauhin, 1650, as "Cucurbita longa, folio molli, flore albo". Fuchs' "Cucurbita maior"

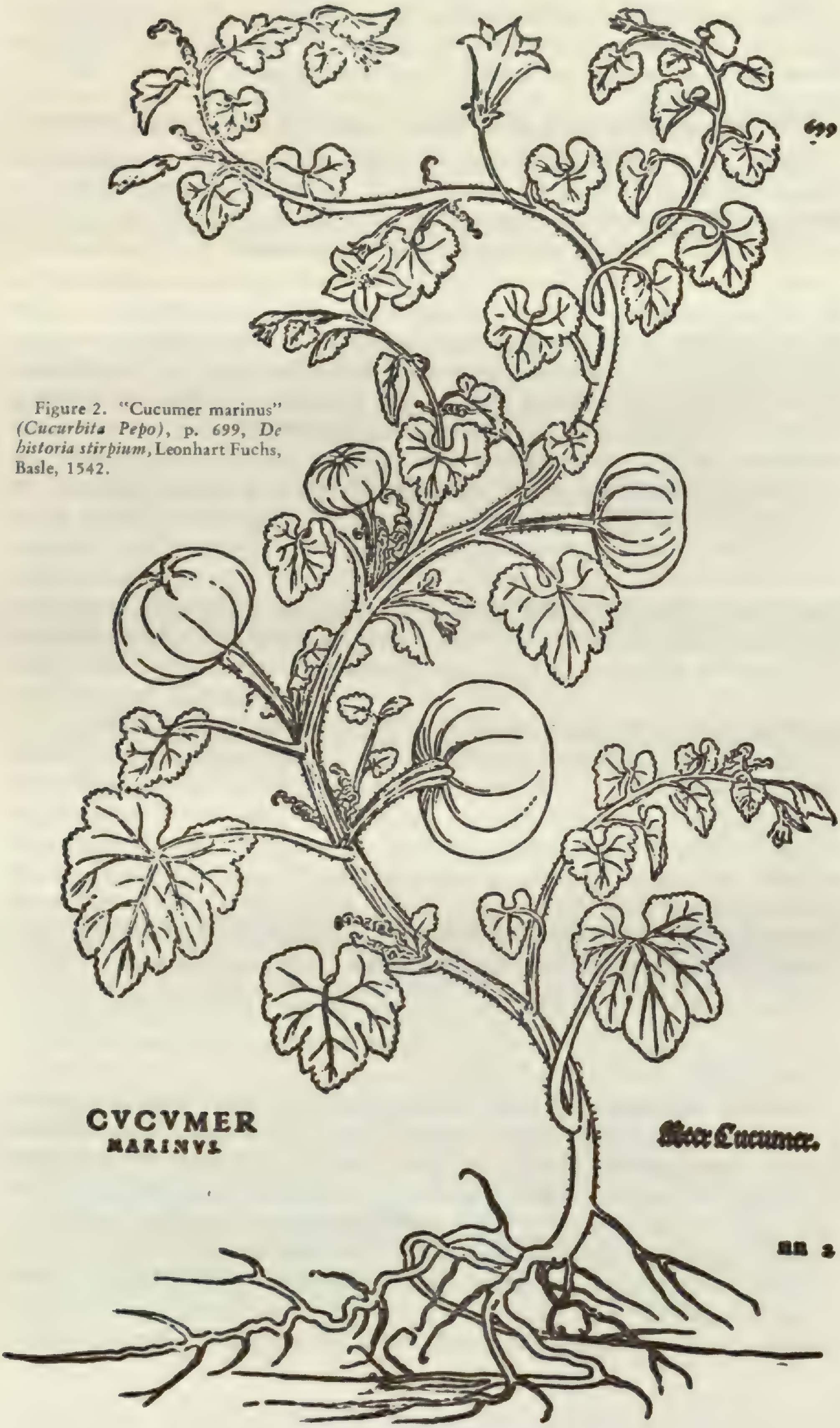

Figure 2. "Cucumer marinus" *(Cucurbita Pepo)*, p. 699, *De historia stirpium*, Leonhart Fuchs, Basle, 1542.

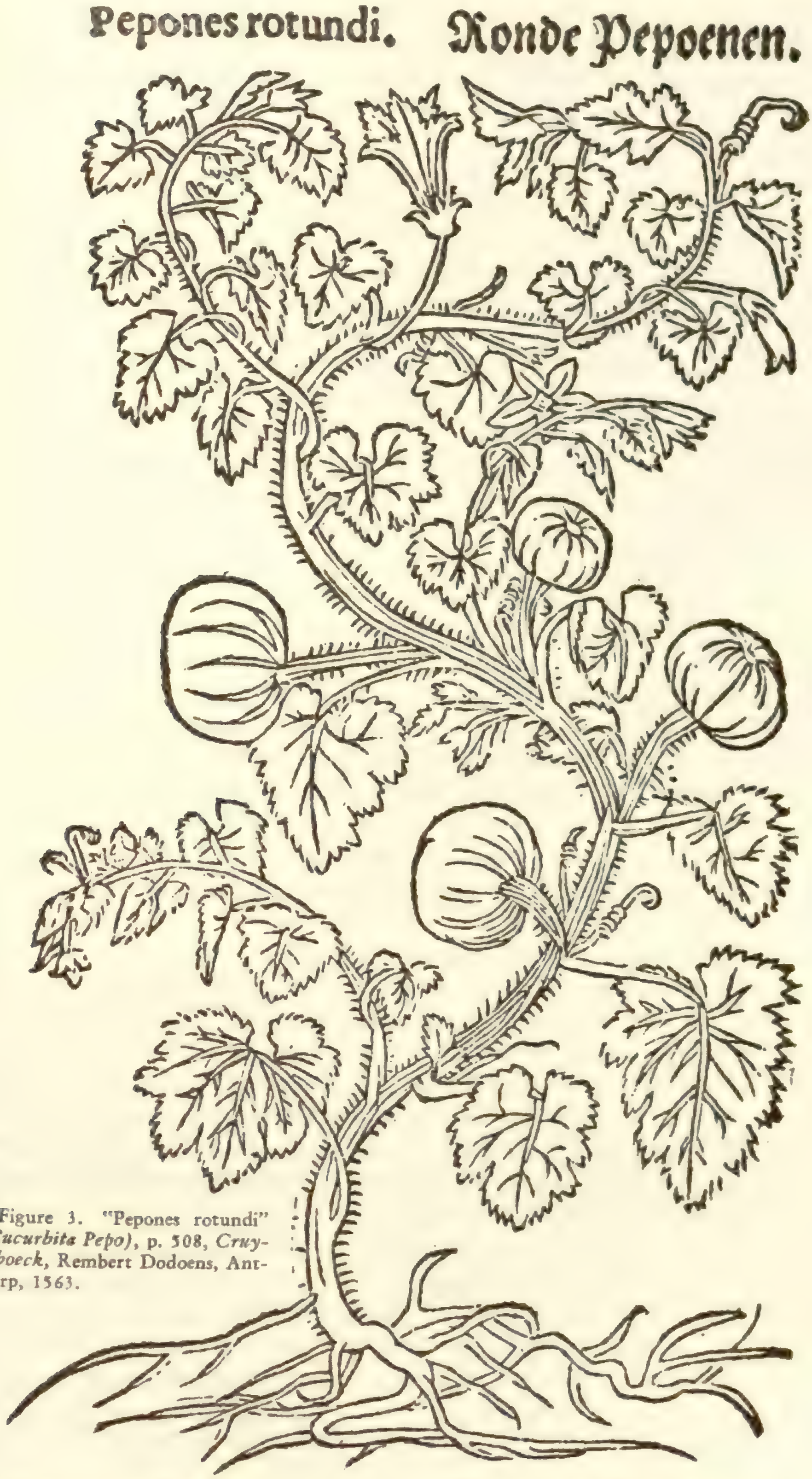

Figure 3. "Pepones rotundi" (*Cucurbita Pepo*), p. 508, *Cruydeboeck*, Rembert Dodoens, Antwerp, 1563.

reappears in Dodoens in 1563 as "Cucurbita cameraria maior", which Dalechamps also called it in 1587. (His plate, however, is a reverse of Dodoens', with slightly different measurements.) Gerarde (1636) seems to have used Dodoens' block, calling it "Cucurbita lagenaria", and in 1650 Bauhin brings it to a small, inglorious end, again, as "Cucurbita latior folio molli, flore albo". Fuchs' third and last *Lagenaria* was called "Cucurbita minor", and Dodoens (1563) called it by the same name. In 1587 it became "Cucurbita cameraria minor" in Dalechamps, and in 1650 "Cucurbita lagenaria" in Bauhin. Obviously, there was some confusion in nomenclature! All of the Dodoens illustrations are approximately the same size as the cuts of Fuchs' 1545 edition, and possibly from the same blocks. Dalechamps' cuts are slightly smaller and all but the "Cucumer marinus" derivative in reverse of the above, so he cannot have used the originals; Gerarde's print is clearer than Dodoens', but may be from the same cuts. The cuts used by Bauhin are all smaller and *far* coarser than any of the others.

However, not all the wood cuts used in the herbals of the period after Fuchs derive from him. A cut called "Pepones lati" in 1563 and "Pepo latus" in 1616 by Dodoens is used again by Gerarde in 1636 as "Pepo Indicus angulosus", and identified by Whitaker (1947) as "*C. Pepo*, possibly var. White Bush Scallop". Again, Dalechamps in 1587 published a charming decorative print of "Cucurbita verrucosa" with a good deal of fine, accurate detail, identified by Whitaker as "evidently a warted variety of *C. Pepo*". The same material, cut down in size, in mirror image, with far less grace and detail, was published by Bauhin (1650) as "Cucurbita verrucosa" and cited by Linnaeus, in 1753, in *Species plantarum* in his definition of "Cucurbita verrucosa". (But Linnaeus added, in later editions, that the plant bore marked resemblances, in flowers and seeds especially, to *C. Pepo*.) This is another example of the enormous botanical value of even such a coarse, much-worried hand-me-down as Bauhin's figure, especially as, according to Bailey (1929) the Linnaean herbarium contains no specimen named "Cucurbita verrucosa" by Linnaeus.[12]

In 1576 (*Plantarum seu stirpium historia*) and 1591 (*Icones stirpium*) L'Obel published as "Pepo maximus Indicus compressus" a cut identified by Whitaker (1947) as the first illustration of *Cucurbita maxima*. In 1587 Dalechamps used the picture in mirror image, as "Pepo maximus Indicus, L'Obel"; his cut measures 12 × 7 cms., a bit smaller than the one used by L'Obel, by Dodoens as "Pepo rotundus maior" in 1616, and again in 1636 by Gerarde, as "Pepo maximus compressus". This cut (referred to L'Obel) is cited by Lamarck in his *Encyclopédie*, ii, 151 (1786). Bauhin is also cited by Lamarck, for his portrait of "Cucurbita aspera, folio non fisso, fructu maximo, albo sessili".

In 1591 Tabernaemontanus published in his *Neuw Kreuterbuch* as "Pepo Indicus minor angulosus" a cut used by Gerarde in 1597 as "Pepo Indicus angulosus". The print is poor in Gerarde, but the detail in the cut is excellent and is identified by Whitaker (1947) as "probably *C. Pepo*, var. 'Table Queen'". As before, Bauhin has a mirror image of the same cut, in smaller size, and names it as

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[12] In section 1151 of his *Catalogue of the Linnaean Herbarium*, London, 1945, Spencer Savage lists five specimens of the genus, but none is labeled *Cucurbita verrucosa*.

did Tabernaemontanus. The cut is unusual among those of the period in that it does not show a root.

The same authors use another cut, originally described by Tabernaemontanus as "Pepo Indicus minor clypeatus" and by Gerarde (1597) as "Pepo Indicus fungiformis". Again Bauhin's use of it is in mirror image on a smaller scale; he calls it "Cucurbita clypeiformis cortice molli et ramosa" and Bailey (1929) says it is "undoubtedly one of the forms of *Cucurbita Pepo* var. *Melopepo*" although tendrils are a conspicuous part of this figure, and Bailey himself (1954) describes var. *Melopepo* as "Plant covering small space, compact, not running or tendril-bearing". However, this last, negative character is not cited by all authorities.

Again, Tabernaemontanus' "Cucurbita capitata" appears in Gerarde (1597 and 1636) as "Cucurbita sylvestris fungiformis" and in Bauhin (smaller and reversed) as "Cucurbita capitata Tabernomontani sive clypeiformis". This, which bears no tendrils, Bailey (1929) again identifies as *Cucurbita Pepo* var. *Melopepo*.

ICON V.

Figure 4. "Cucurbita foliis asperis sive Zucha flore luteo" *(Cucurbita Pepo)*, vol. II, p. 219, Ic. V, *Historia plantarum universalis*, Johannes Bauhin, Yverdon, 1650–51.

Tabernaemontanus' "Melopepo clypeatus" becomes "Pepo maximus clypeatus" in Gerarde (1597) and (diminished in size and reversed in image) "Cucurbita clypeiformis, sive Siciliana Melopepon latus a nonnullis vocata" in Bauhin. This cut is again without roots; it does, however, show exceptionally good detail of flower and fruit structure and is without tendrils. It is particularly important as it represents another definite citation by Linnaeus in his description of *Cucurbita*, this time "C. Melopepo". Bailey (1929) says "the plant is undoubtedly what we know as Bush Scallop squash".

Bauhin used Tabernaemontanus' "Cucurbita longa" as his "Pepo Indicus minor, Tabern." and Gerarde in 1597 used Tabernaemontanus' "Melopepo compressus" as his "Pepo maximus compressus"; Tabernaemontanus' "Melopepoteres" as his "Pepo maximus rotundus"; and Tabernaemontanus' "Pepo maximus oblongus", as (for once not complicating the problem) "Pepo maximus oblongus".

Gerarde, in 1636, had access to cuts used by L'Obel in 1576 and 1591. L'Obel's "Pepo oblongus vulgatissimus" (1576) became "Pepo oblongus" in 1591, but

Gerarde called it "Pepo maior sylvestris". L'Obel's "Pepo rotundus compressus Melonis effigie" retains its name in both his editions, but Gerarde calls it "Pepo Indicus minor rotundus", and Parkinson (*Theatrum botanicum*) in a *very* coarse 1640 reprint, "Melo Indicus parvus".

The last of the cuts of *Cucurbita,* in Bauhin, makes a very poor print indeed, and must, like the others, have been cut down from another wood block, although I have not found it printed elsewhere. However, it is another important, though indirect, Linnaean reference. Bauhin called it "Cucurbita foliis asperis sive Zucha flore luteo, Ic. I." Linnaeus refers in his *Hortus Cliffortianus*[13] and his *Hortus Upsaliensis* to Ray's *Historia plantarum*[14] which in turn refers to this cut in Bauhin. Bailey (1929) says, "This figure is again *C. Pepo* as we know it".

Gerarde in 1597 used three cuts of *Lagenaria* which had been used previously by Tabernaemontanus. The latter author's "Cucurbita Indica minor" became "Cucurbita anguina" in Gerarde; his "Cucurbita lagenaria minor", "Cucurbita lagenaria sylvestris". In 1636 Gerarde used cuts as "Cucurbita anguina" and "Cucurbita lagenaria sylvestris" which had also been used before and were to be used again. L'Obel (1576 and 1591) had used the first as "Cucurbita sive Zuccha omnium maxima anguina" and Dodoens as "Cucurbita longior". Parkinson apparently used the same plate, in 1640, as "Cucurbita longa." L'Obel also in both his editions used the second of these as, simply, "Cucurbita lagenaria" and Dodoens as "Cucurbita prior". Again, Parkinson apparently used the same plate, this time as "Cucurbita lagenaria maior".

The constant and confusing repetition of these figures is largely due to "pools" of botanical cuts made by the publishers of botanical books. Of these the best known is Christopher Plantin, the great printer of Antwerp. Plantin's firm continued publishing for three hundred years, his place of business becoming a museum in 1876, when it was purchased by the city of Antwerp from the eighth generation of the family Moretus, direct descendants of Plantin's son-in-law, who was also his chief assistant.

Plantin published L'Obel's work as well as the later writing of Dodoens. These two men, along with Charles de L'Ecluse (who apparently used no cuts of the key genera) were friends who worked so closely together that it is not possible to tell which or who was originally responsible for material or figures in their publications.

In 1576 Plantin published *Plantarum seu stirpium icones* using L'Obel's name although many of the cuts had also been used to illustrate the herbals of Dodoens and de L'Ecluse. It is thought that it was this selection of woodcuts which Johnson bought to use in his editions of Gerarde's herbal in 1633 and 1636 (Arber, 1938). Arber (1938) believes this to be the last time the Plantin collection of blocks was used.

Jacques Dalechamps, whose *Historia generalis plantarum* appeared at Lyons in

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[13] "Monoecia syngenesia Cucurbita–g. pl. 738 2. C. seminum margine integro tumido Pepo vulgaris–Raj. hist. 639." (*Hortus Cliffortianus,* Amsterdam, 1737; p. 452.)

[14] "Cap. II. De Pepone. 1. Pepo vulgaris. Cucurbita foliis asperis sive Zuccha flore luteo J. B. . . . The common Pumpion, called by the vulgar, The Melon." (Ray, John, *Historia plantarum,* London, 1686–1704; p. 639.)

1587, and Jakob Tabernaemontanus, whose *Neuw Kreuterbuch* was published in Frankfurt a few years later, both seem somehow to have had access to the Plantin "pool" of cuts, as is evident from the above tracing of relationships to the same figures found in Dodoens and L'Obel; or they used, as did so many others, the octavo blocks from Fuchs' 1545 edition. Arber (1938) says that Tabernaemontanus made a collection of blocks for himself, and that they were acquired from him by John Norton to be used in his 1597 edition (the first) of Gerarde's *Herball*. According to Bartlett (1949) this was based upon a translation of Dodoens' second herbal, begun by a Dr. Priest; Gerarde took over the work for Norton, the publisher, after the death of Dr. Priest, so the material is hardly original. Gerarde is particularly remembered as a horticulturalist, having supervised the care of several famous English gardens and having himself cultivated for twenty years a fine garden of his own in Holborn.

Although John Parkinson also had a famous London garden, and was known as "Herbarist to Charles I", the examples of illustrations of my key genera found in his *Theatrum botanicum* leave much to be desired.

Other Woodcuts in Herbals of Sixteenth and Seventeenth Centuries

The search for "icones" of the key genera takes us now to Padua, where in 1638, appeared a little book on the plants of Egypt. The woodcuts of *Luffa* used by Vesling (*De Plantis Aegyptiis*, 1638) are highly stylized and poorly printed, and are not included as illustrations in Alpino's original (1592) edition of the book to which Vesling is supposedly only adding "observationes et notae". However, Sims, who edited the 1814 volume of the *Botanical Magazine*, thought rather highly of Vesling's cut. "Professor Cavanilles", Sims wrote in connection with Plate 1638, "supposes that 'Momordica Luffa' of Linnaeus may probably belong to the same genus (*Luffa*). Indeed these two plants appear to be extremely similar, as we judge from the excellent figures of Veslingius [sic], in his observations on Prosper Alpino".

Most of the seventeenth century botanical books, however, differ from Vesling in that they reflect the stimulus which all the natural sciences received from the discovery of the New World. The earliest of these that falls within the limits of this paper appeared in Amsterdam in 1648, the *Historia Naturalis Brasiliae*. The author of the section entitled *Historia Rerum Naturalium* was Georg Marcgrave, who had accompanied a Dutch expedition which conquered Brazil and took it briefly from the Portuguese. According to Wm. Swainson (1834), "Marcgrave's work abounds with a vastness of new and original information, very different from what was to be found in the crude and verbose compilations of this period." He has left for us a small wood-cut of *Fevillea*, and several other cuts which are apparently of members of the Cucurbitaceae, but are too crude and rough to be recognizable. The cut of *Fevillea* most certainly does not fit my definition of "icones", but like those of many of the herbalists it has value because of the time and place it was made. The same cut is found again in Piso's *De Indiae utriusque*, Amsterdam, 1658, actually the second edition of the volume listed above. The work of Marcgrave and Piso is so inextricably entangled that it is impossible to

know who is responsible for what. The editor of the 1648 edition gave credit to both (after Marcgrave's death), but Piso took all the credit for the second edition unto himself. The credit for the illustrations, however, is of dubious value, as Nissen (1951) writes, in his inimitable Teutonic verbosity, that "the cuts are in no way suitable to verify a doubt-free determination of a specific object".

Engravings

The decadence into which the botanical woodcut sank after reaching a high in Fuchs' herbal has been traced through a devious history; with the introduction of metal plate incision comes another breath of good fresh air. This introduction presents a second of the strange anachronisms in the history of botanical illustration, comparable to the generally poor plant portrayals in the printed herbals during a period when beautiful flower paintings were being made.

The technique of engraving on metal stems from the great goldsmith tradition of the artisans and was translated to the graphic arts sufficiently early to have reached a high point in the works of Martin Schoengauer, 1445–91. However, the earliest strictly botanical book containing illustrations printed from metal plates did not appear until a century after Schoengauer's death (Van Schaack, 1959). This was Fabius Columna's *Phytobasanos*; it contained no pictures of my selected Cucurbitaceae, nor have I found such pictures in books printed until a hundred years later still. This fact, however, gives a falsely exaggerated impression of delayed adaptation of the new technique to botanical illustration. After the publication of Columna's etchings, the makers of botanical prints finally recognized that the incision of metal plates permits a far more delicate line than does woodcutting, and the genus flourished through the seventeenth century.

Between 1678 and 1703 appeared the 12 folio volumes of *Hortus indicus malabaricus*, copiously illustrated with double page copper engravings, by Heinrich Adrian van Rheede tot Draakestein, and containing "icones" of *Cucurbita moschata*, *Lagenaria vulgaris* (see plate XIV), *Luffa acutangula* and *L. cylindrica*. Malabar lies on the west coast of southern India, and Rheede was governor of the province. Blunt (1951) feels that the author may himself have had a part in making the drawings of plants, though the plates were engraved by an Italian monk, Father Mathieu. The illustrations are sometimes of immature plants and sometimes (like those of Weiditz) picture in close detail the flaws of individual specimens, but their large size and strong calligraphic quality give them a vitality which many other plant illustrations lack. This is one of the best known of the pre-Linnean botanical books which reflect the stimulus of the introduction into Europe of new plants found during voyages of exploration or scientific inquiry. The works of Commelin, Rumpf and Plumier (see below) fit into this same category, Rheede, Commelin and Rumpf particularly pointing up, as Blunt (1951) reminds us, "the interest shown by the Dutch in the flora of their colonial possessions."

Commelin's book, *Horti medici Amstelaedamensis*, concerns the rare and exotic plants in this Physic Garden, with illustrations drawn from life. These include a *Luffa operculata*, typical of the stiff engravings taken from paintings by Johan

and Maria Moninckx, to which originals Blunt (1951) claims that justice is not done. Caspar Commelin, the author, was a professor of botany and the nephew of Jan Commelin, who had been director of the Physic Garden.

The next illustrations of the key genera appear in the 6 volumes of Georg Eberhard Rumpf's *Herbarium Amboinense* published, again in Amsterdam, between 1741 and 1750. The story of the author's life is a series of mishaps so catastrophic that one can only wonder that his work was *ever* published. Rumpf became an employee of the Dutch East India Company in 1652, and settled at Amboina[15] where he indulged his love of nature until he died in 1702. However, fire, shipwreck and blindness all tested Rumpf's patience and courage, so that one cringes from criticism of the illustrations of *Cucurbita* (*C. Pepo* and *C. moschata*), *Lagenaria* and *Luffa* (*L. acutangula* and *L. cylindrica*) in his book. Let me only say that their quality is extremely variable, due to the fact that Rumpf's drawings from which his descriptions were made, were burned and he became blind before he could make more. Hence several people, including his son, made the new set, in many of which the botanical detail is poor. However, the books remain important because later authors have used his descriptions and figures as the types of many binomials of plants of the Malay flora (Merrill, 1917).

Plantarum americanarum listed hereafter as containing "icones" was published in Amsterdam between 1755 and 1760, and was edited by Burmann, a well-known professor of botany in that city. Burmann's "last labor" (*General Biographical Dictionary*, 1813) was to procure "engravings to be executed for the drawings of American plants left by Plumier, to which he added descriptions". Plumier, a member of a French religious order, had been sent to explore the French settlements in the West Indies, and succeeded so well that he was subsequently appointed botanist to the king (*General Biographical Dictionary*, 1813). He published many of his drawings in Paris in 1693, but these did not include the *Fevilleas* that give him entrée to the list. His plant figures were drawn to large scale in bare, cold outline, and have little artistic merit; but they were often referred to by Linnaeus, who had access to a set of copies at the University of Groningen (Sitwell and Blunt, 1956).

The next book (*Histoire universelle du regne végétal* by Pierre Joseph Buch'oz, 1775–80) containing an illustration (*Cucurbita Pepo*) that falls within the limits of this paper is the work of a botanical artist of mixed repute. Buch'oz' works are listed by Sitwell and Blunt, by Dunthorne and in most of the catalogues of exhibits of fine flower books, but the opinion in which he was held by contemporary botanists needs no elaboration beyond the specific epithet "foetida" which L'Héritier applied to a plant of the genus *Buchozia*. Nissen (1951) quotes Pritzel in a brief statement which shows no evidence of Buch'oz' reputation having soared posthumously. "Miserimus compilator", Pritzel called him, "fraude ac ignorantia aeque emineus". Pierre Joseph Buch'oz is credited with having written on all branches of natural science though understanding none, and with compiling some 300 volumes though remaining undistinguished himself! But his illustrations are very attractive indeed and Blunt (1951) grants him a few kind words because he intro-

[15] Amboina is one of the Moluccas in Indonesia.

duced into floral illustration "the decorative qualities which we always associate with Far Eastern art".

Antonio José Cavanilles is quite something else again. Of great botanical interest, his 6 volume *Icones et descriptiones plantarum*, concerning the plants that grew in Spain, either "spontaneously or cultivated in gardens", during his time, contain rather stiff engravings with no oriental charm whatsoever. These books were published at Madrid between 1791 and 1801, and among them is a clean cut of a *Luffa acutangula*.

The engravings of Rheede, Rumpf, Plumier, Buch'oz and Cavanilles were all printed and published in fine, folio volumes, representing "the apogee of the art of botanical illustration, reached in the 18th century" (Mongan, 1952). Next on my list is a group of smaller volumes, all published as handbooks to medical, economic or systematic botany.

The Influence of the Linnaean System

Christian Schkuhr published at Wittenberg, in 1791, 6 octavo volumes of his *Botanisches Handbuch*, the last 3 volumes consisting of an atlas of colored (in the Missouri Bot. Gard. copy) engravings. Nobody but Nissen and I seem to consider him worth mentioning, but I find the engravings both charming and carefully done, and Nissen gives Schkuhr credit for both the drawings and the plates.

Schkuhr's *Handbuch*, post-Linnean, is the first of my list to exemplify the new spirit which entered the study of botany after the publication of the *Species Plantarum* in 1753. Linnaeus' binomial system stimulated revision of older means of plant description and classification, and "called for a new and different type of illustration which emphasized scientific accuracy in the delineation of flower, fruit, leaf and stalk" (Dunthorne, 1938). The wealth of diagnostic detail included in Schkuhr's plate of *Cucurbita Pepo* is an excellent example of this new and different type, and also illustrates Dunthorne's point that "the new scientific artists first appeared in Germany". The particular care taken in dissections of the androecium and gynoecium were of course important, because Linnaeus'[16] sexual system was based on the number of parts included in each of these floral organs.

Mr. Nissen and I are joined by Sitwell and Blunt, and Dunthorne in listing the next entry, Johannes Zorn's *Icones Plantarum Medicinalium*, which also appears in Dutch translation by Dheoderich Leonard Oskamp as *Afbeeldingin der Artseny-gewassen*. The colored engravings of *Lagenaria* are identical in the two editions, and are quite charming.

The next series chronologically on my list is mentioned by Nissen and Sitwell

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[16] Linnaeus' sexual system was introduced in his *Systema Naturae* of 1735; the genera were grouped basically into classes according to their number of stamens, into orders according to their number of pistils. *Cucurbita* comes under Class 21, Monoecia, described as "Mares habitant cum feminis in eadem domo, sed diverso thalamo. Flores masculi et feminei in eadem planta sunt." Besides being monoecious, *Cucurbita* is described as Syngenesia, or "Mariti genitalibus foedus constituerunt. Stamini antheris (raro filamentis) in cylindrum coalita." English translations of Linnaeus' Latin were made in 1783 by "a Botanical Society" with thanks for the help of Dr. Samuel Johnson. These translations appear in the Ray Society's 1957 facsimile edition of Vol. 1 of the *Species Plantarum* in the introductory section, "Linnaeus's Sexual System of Classification", and lead one to suspect the learned doctor of baiting with tongue in cheek those botanists who had earlier described Linnaeus' mathematical system as "lewd" and "licentious".

and Blunt. Published by Ferdinand Bernhard Vietz, 10 quarto volumes including 1086 hand-colored engraved plates, *Icones plantarum medico-oeconomico-technologicarum,* appeared at Vienna between 1800 and 1820. The plate of *Cucurbita Pepo* is large, printed on a folded double page, and has a great deal of charm. A *Lagenaria* plate is also ascribed to Vietz, but it is not included among the volumes (1–3) in the Missouri Botanical Garden library.

I bring in Curtis' *Botanical Magazine* now because its earliest plate of one of the key genera fits chronologically into the list of "icones" at this point. Actually, publication of this splendid serial began in 1787 and has continued almost uninterruptedly until the present day, practically all of its plates being hand-colored until as late as 1948!

William Curtis, Praefectus Horti and Demonstrator to the Society of Apothecaries at Chelsea, founded the magazine to describe and illustrate "the most Ornamental FOREIGN PLANTS", the illustrations to be "always drawn from the living plant". When Curtis died the editorship was taken over by his friend, J. Sims. Sims' plate 1638, published in 1814, gives (as mentioned above) Cavanilles as a reference for his *Luffa acutangula,* a lovely copper engraving, probably by Sansom, from a drawing by Sydenham Edwards. Edwards is described by Blunt (1951) as "Curtis' own creation", as it was Curtis who recognized talent in the son of a Welsh schoolmaster, and brought him to London for instruction. Edwards remained practically the sole illustrator of the *Botanical Magazine* from the publication of the second volume in 1788 until 1815, some years after Curtis' death; he is credited with about 1650 plates!

The only other of the key genera illustrated among the nearly 10,000 plates in the *Botanical Magazine* is a *Fevillea cordifolia,* plate 6356, published in 1878. It presents an interesting contrast to the *Luffa,* as this was a period of low ebb in the printing arts; it is lithographed on poor quality paper, and has none of the charm or calligraphic quality of either earlier or later plates. At this time J. D. Hooker was editor, and it was under him that "the last traces of the Linnaean System vanished from the classification of plants in the *Botanical Magazine*" (Blunt, 1951). Sir Joseph Hooker is best known as an early champion of Darwin and for his botanical explorations, which contributed greatly to the knowledge of plant geography.

W. Fitch, artist of the *Fevillea* plate, was "discovered" by William Hooker, father of Sir Joseph, while the to-be-Director of Kew Gardens was a professor of botany and the to-be-artist an apprentice designer of calico, both in Glasgow (Blunt, 1951). Sir Joseph Hooker, after inheriting this enormously prolific draftsman, described him as an "incomparable botanical artist", with "unrivaled skill in seizing the natural character of a plant". Blunt (1951) finds his work too facile and insensitive, but adds that Fitch "remains the most outstanding botanical artist of his day in Europe", despite the fact that his drawings were made from dried plants. Blunt gives him additional credit as the first artist to be able to do this satisfactorily. Otto Stapf, editor of vols. 148–156 of the *Botanical Magazine,* has given a satisfying explanation of why this was possible:

> "Fitch had a marvelous power of visualizing plants as they lived and retaining their image in his memory. This emboldened him rather to treat his originals as sketches than to work them into finished pictures, with the result that when finally drawn on stone they underwent a certain generalization in which the type of the species came to life and took the place of a photographically true portrait." (Quoted from Blunt, 1951.)

This statement concerning Fitch's method[17] is of interest in relation to my earlier discussion of "icones" as essentially portraits of species rather than of individuals as were the woodcuts of Weiditz.

François Pierre Chaumeton, "docteur en médecine", well understood the value of fine botanical illustration. "There are few sciences", he wrote in the preface to his *Flore Médicale*, 1814–20, "which demand more imperiously than botany, the help of painting. One would have to try very hard indeed to replace it with the most precise description". A doctor with such an opinion would also try very hard indeed to illustrate his book with the most precise drawings, and Chaumeton did just that. His two pictures of *Cucurbita Pepo* were made by P. J. F. Turpin, one of the great botanical draughtsmen of the day. Turpin worked with botanists of the highest caliber, Poiteau and de Candolle, as well as illustrating many of the American plants pictured in Humboldt, Bonpland and Kunth's publication concerning the expedition to the "régions équinoxiales du Nouveau Continent, 1799–1804".[18]

Turpin is described as being largely self-taught, but Blunt (1951) sees in his work "great indebtedness to the tradition of van Spaendonck and Redouté", both artists from whom no follower need feel shame to borrow. Elizabeth Mongan (1952) gives an excellent explanation for this:

> "France became pre-eminent in the art of botanical flower prints at the beginning of the nineteenth century with such artists as Redouté, Prévost, Bessa, Turpin, Poiteau and Madame Vincent. They were all the pupils of van Spaendonck, and the skill of these artists can be attributed almost entirely to the thorough training they had had with such a master, but there was another reason for their ascendancy. This was their use of stipple engraving, a method that made possible color printing *à la poupée*.[19] Such excellence as these artists attained could not have been achieved by the use of the etched or engraved line that necessitated coloring of the print by hand."

Two years after Chaumeton began publishing the various editions of his work (folio, quarto and octavo), publication began, under the general direction of Cuvier,[20] of the *Dictionnaire des Sciences Naturelles*. This was a most ambitious work, appearing in Paris between 1816–30 in 60 volumes of text, with 14 of atlas, and planned (according to the title page) to "treat methodically the various natural beings, from the point of view of our knowledge of them and also relative

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[17] Fitch also published eight interesting articles on the subject of botanical drawing, which appeared in *The Gardeners' Chronicle* in 1869. These elaborate his method in great detail, but contribute nothing new to a discussion of what constitutes living portraits of plants, or "icones".

[18] Among these was a so-called *Fevillea*, but Cogniaux relegated it to the genus *Sicydium*, so the great *Nova genera et species plantarum* (better known as "H.B.K.") of 1815–25 is not included in this discussion.

[19] "That is, the plate was daubed in various colors with tightly knotted cloths, resembling rag dolls *(poupées)* and then the whole thing printed at once." (Van Schaack, 1959.)

[20] Georges Léopold Chrétien Frédéric Dagobert, the Baron Cuvier (1769–1832), was a French zoologist who, among other high positions, held the post of Professor of Comparative Anatomy at the Jardin des Plantes.

to their use in medicine, agriculture, business and the arts". DeJussieu[21] was originally in charge of the botanical section; Turpin of the execution of the drawings and the general direction of the engraving. Unfortunately Turpin made only two plates among the key genera, both of *Fevillea cordifolia* (see plates XII and XIII). Turpin's drawings of botanical detail are generally acknowledged to be exceptionally fine, and these plates well illustrate the fact. One of the plates, for instance, depicts not only a "sterile" (male) flower in natural size, but a view of it from below: the androecium; a single stamen; and a view of *it* from the rear. Equally detailed dissections are made of a "fertile" (female) flower; and, need I add, the habit of the plant is also shown, all in one beautiful, colored, octavo page.

In 1821, M. E. Descourtilz published in Paris his 8 volumes on the *Flore Médicale des Antilles,* an assemblage made while he, a doctor, served in official capacity at Santo Domingo. Descourtilz used illustrations of several of the key genera (*Cucurbita moschata, C. Pepo*—both of which are pictured twice under different names; *Fevillea cordifolia* and *Lagenaria vulgaris*); these pictures have a good deal of charm, but are poor specimens of botanical illustration, despite the fact that the author claims to have drawn them from nature and to have watched his son cut them down in size before painting them with the greatest care. Though the father claims that his son Théodore was a pupil of the "célèbre Wanspaendonck", the slipshod attempt at portrayal of detail is only a sort of casual acknowledgment of its desirability. In contrast to the works of Turpin, these are sad indeed.

Lithographs

The eleven large folio volumes of Velloso's *Florae fluminensis icones,* published in Paris in 1827–32, illustrate the flora of the region around Rio de Janeiro. Velloso was a native Brazilian who became one of the most zealous students of Domenico Vandelli, the Italian botanical explorer, and is thought to have supplied most of the plants described in Vandelli's works (Nissen, 1951).

Velloso must have been an ardent botanist to collect so many plants, but the art work in his book leaves much to be desired. The de Candolles (1878) wrote that "the figures [of *Florae fluminensis*] like those of Plumier, are very bad. The safest thing is to class the species of these authors . . . in a very doubtful category, which one can call *inextricables*". The figures do, however, play some part in the history of the graphic arts as they were lithographed by Senefelder, who discovered the process "almost accidentally" (Blunt, 1951) in 1797. The advantage of lithography, the technique employed in all the remaining "icones" on my list except those of Iinuma and Bailey, is that it permits subtle gradations of line; as is readily seen in his *Fevillea trilobata, Luffa cylindrica* and two *Lagenarias,* however, Velloso did not profit from this opportunity, but drew in bold outline only.

The next "icones" on the list also illustrate Brazilian plants. Karl Friederich Philipp von Martius, a German botanist and traveler, was sent to Brazil in 1817 by the king of Bavaria. He returned to positions at the botanical garden and the university in Munich, where he began work on his *Flora Brasiliensis* in 1840.

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[21] Antoine Laurent de Jussieu (1748–1836) is known as the first taxonomist to present a natural system of plants, actually an improved version of one assembled, but never published, by his uncle, Antoine. In 1793, the younger Antoine founded one of Europe's great museums, the Musée d'Histoire Naturelle de Paris (Lawrence, 1951).

Fifteen volumes in 40 folio parts were published between that date and 1906 in Munich, Vienna and Leipzig, the later volumes, of course, edited by younger men. The 3000 lithographs in the series were made by a number of artists, and include a *Fevillea trilobata* and a *Luffa operculata*, both of which are drawn in unusually fine detail.

Robert Wight's *Icones plantarum Indiae orientalis*, 6 quarto volumes of lithographs published in Madras between 1840 and 1856, contains some of the botanically finest "icones" on my list. The two-page spread of *Cucurbita maxima* includes an extraordinarily complete floral analysis; the *Luffa cylindrica* is done in such detail that one sees even the fine webbing at the edge of the leaf. The two plates, drawn by the Indian artist Rungiah and lithographed by Dumphy, are typical of the work of several generations of talented native artists who worked in India at about this time (Nissen, 1951). Wight, however, was not too happy about the way they were printed, especially in the early volumes. He apologizes in his preface with the explanation that lithography, still in its infancy in Europe, was even more of a fledgling in Madras, where inexperienced printers had not yet learned to compensate for the atmospheric difficulties which affected the success or failure of the plates. Hooker and Thomson (1855) in their Introductory Essay to the *Flora Indica* call Wight's works "the most important contributions not only to Botany, but to Natural Science, which have ever been published in India".

Later Work in Various Techniques

When discussing the botanical woodcuts of the 16th and 17th centuries, I expressed admiration for the manner in which Brunfels' and Fuchs' artists handled them, but welcomed warmly the increased grace and delicacy made possible by the technique of engraving. Now, in the last quarter of the 19th century, we find a series of woodcuts so beautiful and finely made that one is forced to realize (as one always is!) that a great artist in any field surmounts the limitations of his medium. These effusions are aroused by Yokusai Iinuma's *Somoku-dzusetsu* or "Illustrated Flora of Japan". The set at the Missouri Botanical Garden is the second edition, printed at Ogaki in 1874 on rice paper of the highest quality. The set consists of 20 quarto volumes in which the illustrations (*Cucurbita Pepo*, 2 *Lagenaria vulgaris* and *Luffa cylindrica*) of my key genera extend across two pages.

In discussing the beautiful woodcuts of Fuchs, I pointed out that, in black and white, they sometimes appeared to be drawn in too thin outline, having obviously been designed with the intent that they be colored by hand. In these Japanese cuts the opposite is often true; the body of the figure is inked and the line, remaining white, is so fine as to seem almost impossible of achievement. In several of the plates I cite, the enlargements of the anther column and gynoecium are printed in color. Nissen, the verbose and usually all-seeing, only notes the *Somoku-dzusetsu* in a list for which he expresses gratitude to others; and, to my surprise, Blunt (1951) says only that it is illustrated with "effective woodcuts".

Manuel Blanco, in the third edition of whose *Flora de Filipinas* we find a *Cucurbita Pepo* and two *Luffas* (*L. acutangula* and *L. cylindrica*), was an Augustinian monk with no training whatsoever in botany, and a botanical library con-

sisting only of one volume of Linnaeus. Hooker and Thomson (1855) in their Introductory Essay call his first edition of 1837 a "botanical curiosity", a statement which covers its reception in Europe, though it met with great local acclaim. Neither the first nor the second edition was illustrated. The third is the work of Fathers Celestino Fernandez Villar and Andres Naves, whose only contribution, according to Merrill (1918), is their Latin translations which made Blanco's Spanish descriptions more generally accessible. The identifications of the plates (drawn by F. Domingo and lithographed by C. Verdaguer) show many errors, a large number of them referring to species which Blanco had never seen. None of the plates of the key genera falls within this category, however. Nissen (1951) goes so far as to damn the illustrations of this deluxe edition by praise so faint it hardly fits the definition. Neither the drawings nor their lithographic reproductions, he felt, compare with the quality of "the old work", but must be compared with their contemporaries, all, by inference, very bad indeed.

Field and Garden Crops of Duthie and Fuller, published in Roorkee in 1882–93, is not mentioned by Blunt or Nissen, nor do its illustrations appear in any of the exhibition catalogues, but the lithographs of *Cucurbita moschata, Lagenaria vulgaris* and *Luffa cylindrica,* albeit utterly lacking in artistic pretension or value, merit place in my list through their other qualifications. The artist of the plates, H. Hormusji, a Parsee imported from the Bombay School of Art, drew the botanical details with great care, and, though they are not pretty, his pictures are surely portraits of living plants. J. F. Duthie was Superintendent of the Saharanpur Botanical Gardens; J. B. Fuller, Director of Agriculture and Commerce for the Northwestern Provinces and Oudh.

Carlos Bettfreund's 3 octavo volumes, *Flora Argentina,* published in Buenos Aires between 1898 and 1901, deal with the "plantas vivas" of Argentina, and are illustrated in the manner of the period, with poorly colored lithographs of no artistic, but presumably some botanical value. These include a *Cucurbita Pepo* and a *Lagenaria vulgaris.* The same criticism may be leveled at F. Gagnepain's section on the Cucurbitaceae in Lecomte's *Flore Générale de l'Indo-Chine,* published in Paris in 1921. This contains a *Luffa cylindrica* drawn, according to the plate, by Mlles. Vesque. I find no mention of this name elsewhere, presumably because the quality of work does not redound to the glory of the artists.

My criteria for "icones" have had to be as much contorted to include the last two publications, as they were also to stretch across the post-Fuchsian herbals. Now they can return to their original shape, though they must, perhaps, still retain a fair amount of elasticity. Engler's *Das Pflanzenreich* would not be found on library shelves under the heading of "icones", nor would its many volumes find their way into the collection of a bibliophile. They do contain, however, besides the most universally accepted system of plant classification, a number of fine drawings of plants. Of the key genera, only a *Fevillea trilobata* appears on a full page and includes the habit of the plant, but I am grateful for it, because it is the best of its type of illustration, apparently the closest we will come, in our time, to fulfilling the criteria for "icones". The *Fevillea* plate contains precise and accurate botanical detail and, though not showy in the slightest lampshadish way, gives a

very pleasant impression of being a portrait of a living plant. This opinion is blessed by Blunt (1951), who points out that many of the illustrations used by Engler, the "greatest of German taxonomists" were unsigned works of Joseph Pohl, whose drawings were "conscientious, accurate, useful and in great quantity, but not on a high artistic level". Of even more significance in these, our troubled times, is the fact that they were made from specimens in the Berlin Herbarium, subsequently destroyed during World War II.

A full-page illustration of *Fevillea cordifolia* in Rendle's *Classification of Flowering Plants* squeezes in among the "icones" by the same reasoning as does Engler's *F. trilobata*. The picture is in Rendle's second volume, which did not appear until 1925, although the first was published in 1904, at which time the material for the second was "almost finished" (Burkill, 1938). It is impossible, therefore, to know if I have placed the book in proper chronological sequence. For our purposes, however, it is only important that we have here again a carefully drawn plant portrait, containing details acceptable to a distinguished taxonomist. Rendle joined the Department of Botany at the British Museum at the age of twenty-three, in 1888, and remained there for fifty years, pursuing, according to his "keen conception of his duty", his work in systematics. Burkill (1938) further describes him as one of those "ships which, as they leave port, have their course set for the whole voyage". He held many botanical posts of honor and responsibility, but his interest was always directed toward taxonomy.

L. H. Bailey's *Garden of Gourds*, a quarto volume issued in New York in 1937, is illustrated with a number of zincograph black and white plates mechanically reproduced from pen and ink drawings. Again, they are of no artistic value, but are pleasing and contain fine botanical detail acceptable to the author, an acknowledged authority on cultivated plants. Of the many illustrations of key genera printed in Bailey's book, I have listed as "icones" only those which best give an impression of habit: "Wild Texas Gourd", "Egg Gourd", "Apple Gourd", "Big Bell Gourd" and "White Pear Gourd", all belonging to the species *Cucurbita Pepo*, var. *ovifera*; *Lagenaria vulgaris* or *Luffa cylindrica*.

Conclusion

Bailey's book contains the last of my "icones", representing well a type of illustration with which it seems that we must learn in these latter days to satisfy ourselves. Botanically they are, of course, authoritative, but they grade very low on the artistic scale, as do all the last group listed. Actually there have been very few on my list that rate high both artistically and botanically, but it must be remembered that this is probably because the key plants do not appeal as floral décor, and have not posed for most of the best-known botanical artists.

Of the publications listed, only Fuchs in the 16th century and Rheede in the 17th contain "icones" that completely fulfill the requirements of my definition—size, habit, botanical accuracy and artistic value; Rumpf, Plumier, Buch'oz and Cavanilles in the 18th century meet the criteria in varying degree, all being at the very least large, fine books from the bibliophile's point of view.

Schkuhr, Zorn, Vietz, Curtis' *Botanical Magazine*, Chaumeton, the *Diction-*

naire des Sciences Naturelles and Descourtilz are less pretentious publications of the late 18th and early 19th centuries, with the happy artistic addition of color, again complying with my requirements to some degree.

Velloso and Martius return to the grand scale, but are more pretentious than beautiful, and poor Velloso is also not held in very high botanical esteem. From these two on, except for the Japanese work of Iinuma, the artistic measure must be dropped entirely, or my list would have to end. I cannot describe Bailey's book (more attractive at least than the others) by even so slight a word of praise as charming, and there is no more temptation to use his illustrations than Engler's or Rendle's on my lamps. This may be a good thing; if the paper is of decent quality, the bookworms stay away, and if anybody supports our libraries, the books may be preserved, as books, for posterity. Though beauty is no longer important in these publications, botanical accuracy is a sine qua non; for this reason and with the message of Dr. Trelease still in mind, we can feel sure that they will serve the purposes of mankind for a very long time to come.

For the sake of consistency in the following indices I have employed the spelling of authors' names used by Nissen (1951), because his bibliography is the most complete I have found. This has led to one or two unfamiliar spellings, as "Karl von Linné" and "Rumpf". Consequently, I have used the name "Linnaeus" in the text, as it is the familiar form in American botany.

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Chronological Index of "Icones" of Key Species

Cucurbita foetidissima:

1552, *Badianus Manuscript:* "Ayonelhuatl", p. 193, pl. 109.

Cucurbita maxima:

1576, L'Obel: "Pepo maximus Indicus compressus", p. 365.
1587, Dalechamps: "Pepo maximus Indicus, L'Obel", vol. I, p. 626.
1591, L'Obel: "Pepo maximus Indicus compressus", p. 641.
1616, Dodoens: "Pepo rotundus maior", p. 666.
1636, Gerarde: "Pepo maximus compressus", p. 920.
1650, Bauhin: "Cucurbita aspera, folio non fisso, fructu maximo, albo sessili", vol. II, p. 221.
1800, Vietz: "Cucurbita Pepo", vol. II, p. 80, pl. 148 (double page).
1840, Wight: *C. maxima,* vol. II, pl. 507 (double page).

Cucurbita moschata:

1678, Rheede: "Schakeri-Schora", vol. VIII, pl. 2.
?1741, Rumpf: "Cucurbita Indica vulgaris, Pepones Labo", vol. V, p. 399, pl. 145.
1821, Descourtilz: "Courge Giraumon à Verrues", vol. V, p. 74, pl. 322; and "Courge Giraumon Veine", vol. V, p. 79, pl. 323.
1882, Duthie and Fuller: *C. moschata,* vol. II, pls. 58 and 59; and *C. moschata, var.,* vol. II, pls. 60 and 61.

Cucurbita Pepo:

1542, Fuchs: "Cucumis Turcicus", p. 698; and "Cucumer marinus", p. 699.
1545, Fuchs: "Cucumis Turcicus", p. 402; and "Cucumer marinus", p. 403.
1558, Matthiolus: "Zucche Indiane", p. 292.
1560, Matthiolus: "Cucurbita Indica", p. 292.
1563, Dodoens: "Pepones lati", "Pepones rotundi" and "Pepones magni", p. 508.
1576, L'Obel: "Pepo oblongus vulgatissimus" and "Pepo rotundus compressus, Melonis effigie", both on p. 365.
1587, Dalechamps: "Cucurbita Indica rotunda", vol. I, p. 616; "Cucurbita Indica longa" and "Cucurbita verrucosa", vol. II, p. 612.
1591, Tabernaemontanus: "Pepo maximus oblongus", "Melopepo compressus" and "Melopepoteres", vol. II, p. 178; "Pepo Indicus minor angulosus", vol. II, p. 179; "Cucurbita longa", vol. II, p. 182.
1591, L'Obel: "Pepo oblongus", p. 641; "Pepo rotundus compressus, Melonis effigie", p. 642.
1597, Gerarde: "Pepo maximus rotundus" and "Pepo maximus oblongus", p. 773; "Pepo maximus compressus" and "Pepo Indicus angulosus", p. 774.
1616, Dodoens: "Pepo maior oblongus", p. 665; "Pepo rotundus minor" and "Pepo latus", p. 666.
1636, Gerarde: "Pepo maximus oblongus", p. 919; "Pepo Indicus angulosus" and "Pepo Indicus minor rotundus", p. 920; "Pepo minor sylvestris" and "Pepo maior sylvestris", p. 922.
1640, Parkinson: "Melo Indicus parvus", p. 772.
1650, Bauhin: "Cucurbita foliis asperis sive Zucha flore luteo, Ics. I, II, III, IV, V", vol. II, p. 218–219; "Pepo Indicus minor angulosus, Tabern.", vol. II, p. 226; "Pepo Indica minor Tabern.", vol. II, p. 227; "Cucurbita verrucosa", vol. II, p. 222.
?1741, Rumpf: "Cucurbita Indica vulgaris, Pepones Labo", vol. V, p. 399, pl. 145.
1775, Buch'oz: *C. Pepo,* Decad. 7, pl. 2.
1814, Chaumeton: "Citrouille", vol. III, pl. 123 and 123 bis.
1821, Descourtilz: "Courge patisson", vol. V, p. 82, pl. 324; "Courge Pepon", vol. V, p. 89, pl. 326.
1874, Iinuma: *C. Pepo,* vol. II, pl. 43 and 43 bis.
1877, Blanco: "Cucurbita sulcata or maxima", atlas II, pl. 320.
1898, Bettfreund: "Cucurbita lagenaria", vol. II, p. 123.

C. Pepo, var. ovifera:

1791, Schkuhr: "Cucurbita ovifera", vol. VI, pl. 314.
1937, Bailey: "Wild Texas Gourd", p. 5; "Egg Gourd", p. 7 and 11; "Apple Gourd", p. 13; "Big Bell Gourd", p. 29; and "White Pear Gourd", p. 33.

C. Pepo, var. Melopepo:

1591, Tabernaemontanus: "Melopepo clypeatus", vol. II, p. 178; "Pepo Indicus minor clypeatus", vol. II, p. 179; "Cucurbita capitata", vol. II, p. 181.
1597, Gerarde: "Pepo maximus clypeatus", p. 774; "Pepo Indicus fungiformis", p. 775; "Cucurbita sylvestris fungiformis", p. 779.

1636, Gerarde: "Cucurbita sylvestris fungiformis", p. 924.
1650, Bauhin: "Cucurbita clypeiformis cortice molli, et ramosa", "Cucurbita capitata Tabernomontani sive clypeiformis", vol. II, p. 225; "Cucurbita clypeiformis sive Siciliana, Melopepon latus a nonnullis vocata", vol. II, p. 224.

Fevillea cordifolia:

1755, Plumier: "Fevillea foliis cordatis", p. 203, pl. 209.
1816, *Dictionnaire des Sciences Naturelles:* "Fevillea hederacea, Poir.", vol. LXIII, pl. 210 and 211.
1821, Descourtilz: "Nandhirobe à Feuilles de Lierre", vol. II, p. 216, pl. 198.
1925, Rendle: *Fevillea cordifolia,* vol. II, p. 222.

Fevillea cordifolia, var. hederacea:

1755, Plumier: "Fevillea foliis trilobis", p. 204, pl. 210.

Fevillea Moorei:

1878, Curtis' *Botanical Magazine*: *F. Moorei* Hook, 3rd series, vol. XXXIV, 1878, pl. 6356.

Fevillea trilobata:

1648, Marcgrave-Piso: "Ghandiroba vel Nhandiroba", Lib. I, p. 46.
1658, Piso: "Nhandiroba", Cap. LXVI, p. 259.
1827, Velloso: "Fevillea cordifolia", vol. X, pl. 102.
1878, Martius: *F. trilobata,* vol. VI, pt. 4, pl. 37.
1916, Engler: *F. trilobata,* vol. IV, 275, I, p. 6.

Lagenaria vulgaris:

1542, 1545, Fuchs: "Cucurbita maior", pp. 368 and 209, resp.; "Cucurbita minor", pp. 369 and 210, resp.; "Cucurbita oblonga", pp. 370 and 211, resp.
1563, Dodoens: "Cucurbita cameraria maior" and "Cucurbita minor", p. 511; "Cucurbita anguina", p. 512.
1576, L'Obel: "Cucurbita sive zuccha, omnium maxima anguina", and "Cucurbita lagenaria", p. 366.
1587, Dalechamps: "Cucurbita cameraria minor" and "Cucurbita cameraria maior", vol. I, p. 616.
1591, L'Obel: "Cucurbita sive zuccha omnium maxima anguina" and "Cucurbita lagenaria", p. 644.
1591, Tabernaemontanus: "Cucurbita lagenaria maior", vol. II, p. 181; "Cucurbita Indica minor" and "Cucurbita lagenaria minor", vol. II, p. 182.
1597, Gerarde: "Cucurbita anguina" and "Cucurbita lagenaria", p. 777; "Cucurbita lagenaria sylvestris, p. 779.
1616, Dodoens: "Cucurbita prior", p. 668; "Cucurbita longior" and "Cucurbita latior", p. 669.
1636, Gerarde: "Cucurbita lagenaria" and "Cucurbita anguina", p. 923; "Cucurbita lagenaria sylvestris", p. 924.
1640, Parkinson: "Cucurbita lagenaria maior" and "Cucurbita longa", p. 769.
1650, Bauhin: "Cucurbita longa, folio molli, flore albo", vol. II, p. 214; "Cucurbita latior folio molli, flore albo", vol. II, p. 215; "Cucurbita lagenaria", vol. II, p. 216.
1678, Rheede: "Bela-Schora", vol. VIII, pl. 1; "Caca Palam", vol. VIII, pl. 4; "Caipa Schora", vol. VIII, pl. 5.
1741, Rumpf: "Cucurbita lagenaria", vol. V, p. 398, pl. 144.
1779, 1796, Zorn-Oskamp: "Cucurbita lagenaria", vol. VI, pl. 597 and 598 and vol. IV, pl. 320 and 321, resp.
1821, Descourtilz: "Courge calebasse", vol. V, pl. 325.
1827, Velloso: "Cucurbita lagenaria", vol. X, pl. 98; "Cucurbita Pepo", vol. X, pl. 100.
1874, Iinuma: "Lagenaria Dasistemon Miq.", vol. XX, pl. 44; "Lagenaria vulgaris, Ser.", vol. XX, pl. 45.
1882, Duthie and Fuller: *Lagenaria,* vol. II, pl. 48.
1898, Bettfreund: *Lagenaria vulgaris,* vol. I, p. 58.
1937, Bailey: *Lagenaria,* p. 93.

Luffa acutangula:

1678, Rheede: "Picinna", vol. VIII, pl. 7.
1741, Rumpf: "Petola bengalensis", vol. V, p. 408, pl. 149.
1791, Cavanilles: "Luffa foetida", vol. I, pl. 9 and 10.
1814, Curtis' *Botanical Magazine*: "Luffa foetida", 1st series, vol. XXXIX, 1814, pl. 1638.
1877, Blanco: "Cucumis acutangulis", atlas II, pl. 288.
1882, Duthie and Fuller: *L. acutangula,* vol. II, pl. 62.

Luffa cylindrica:

1638, Vesling: "Luffa Arabum, seu Cucumis retici latus Aegyptius", pp. 50 and 51.
1678, Rheede: "Catu picinna", vol. VIII, pl. 7.
1741, Rumpf: "Petola sylvestris", vol. V, p. 410, pl. 150; "Petola Tschina", vol. V, p. 406, pl. 147.
1827, Velloso: "Momordica carinata", vol. X, pl. 97.
1840, Wight: "Luffa pentandra", vol. II, pl. 499.
1874, Iinuma: "Luffa petola, Ser.", vol. XX, pl. 36.
1877, Blanco: "Luffa petola", atlas II, pl. 334.
1882, Duthie and Fuller: "Luffa Aegyptiaca", vol. II, pl. 63.
1907, Lecomte: *L. cylindrica,* vol. II, p. 1074.
1924, Engler: *L. cylindrica,* vol. IV. 275. II, p. 66.
1937, Bailey: *L. cylindrica,* p. 105.

Luffa echinata:

1924, Engler: *L. echinata,* vol. IV. 275. II, p. 70.

Luffa operculata:

1706, Commelin: "Momordica Americana Fructu Reticulata Sicco", fig. 22.
1878, Martius: *L. operculata,* vol. VI, pt. 4, pl. 1.
1924, Engler: *L. operculata,* vol. IV. 275. II, p. 70.

INDEX, BY KEY SPECIES, OF WOODCUTS DERIVED FROM ONE SOURCE AND USED BY SEVERAL AUTHORS

("Mirror image" prints are reverse of earliest listed use of figure.)

Cucurbita maxima:

1. 1576, L'Obel: "Pepo maximus Indicus compressus"; 7 × 13 cms.
   1587, Dalechamps: "Pepo maximus Indicus, L'Obel"; 7 × 12 cms.; mirror image.
   1591, L'Obel: "Pepo maximus Indicus compressus"; 7 × 13 cms.
   1616, Dodoens: "Pepo rotundus maior"; 7 × 13 cms.
   1636, Gerarde: "Pepo maximus compressus"; 7 × 13 cms.
   1650, Bauhin: "Cucurbita aspera, folio non fisso, fructu maximo, albo sessili"; 4½ × 8½ cms.; mirror image.

Cucurbita Pepo:

1. 1542, Fuchs: "Cucumer marinus"; folio page.
   1545, Fuchs: "Cucumer marinus"; octavo page; mirror image.
   1558, Matthiolus: "Zucche Indiane"; 12 × 6½ cms.
   1560, Matthiolus: "Cucurbita Indica"; 12 × 6½ cms.
   1563, Dodoens: "Pepones rotundi"; 12 × 7 cms.; mirror image.
   1587, Dalechamps: "Cucurbita Indica rotunda"; 12 × 7 cms.; mirror image.
   1616, Dodoens: "Pepo rotundus minor"; 12 × 7 cms.; mirror image.
   1636, Gerarde: "Pepo minor sylvestris"; 12 × 7 cms.; mirror image.
   1650, Bauhin: "Cucurbita foliis aspersis sive Zucha flore luteo, Ic. V"; 8½ × 4½ cms.
2. 1542, Fuchs: "Cucumis Turcicus"; folio page.
   1545, Fuchs: "Cucumis Turcicus"; octavo page; mirror image.
   1563, Dodoens: "Pepones magni"; 12 × 7 cms.; mirror image.
   1587, Dalechamps: "Cucurbita Indica longa"; 12 × 6½ cms.
   1616, Dodoens: "Pepo maior oblongus"; 12 × 7 cms.; mirror image.
   1636, Gerarde: "Pepo maximus oblongus"; 12 × 7 cms.; mirror image.
   1650, Bauhin: "Cucurbita foliis asperis sive Zucha flore luteo, Ic. II"; 8½ × 4½ cms.
3. 1563, Dodoens: "Pepones lati"; 13 × 7½ cms.
   1616, Dodoens, "Pepo latus"; 13 × 7½ cms.
   1636, Gerarde: "Pepo Indicus angulosa"; 13 × 7½ cms.
4. 1576, L'Obel: "Pepo oblongus vulgatissimus"; 13 × 7 cms.
   1591, L'Obel: "Pepo oblongus"; 13 × 7 cms.
   1636, Gerarde: "Pepo maior sylvestris"; 13 × 7 cms.
5. 1576, L'Obel: "Pepo rotundus compressus Melonis effigie"; 13 × 7 cms.
   1591, L'Obel: as above.
   1636, Gerarde: "Pepo Indicus minor rotundus"; 13 × 7 cms.
   1640, Parkinson: "Melo Indicus parvus"; 13 × 7 cms.
6. 1587, Dalechamps: "Cucurbita verrucosa"; 11 × 6½ cms.
   1650, Bauhin: "Cucurbita varrucosa"; 8½ × 4½ cms.; mirror image.

7. 1591, Tabernaemontanus: "Cucurbita longa"; 12 × 7½ cms.
   1650, Bauhin: "Pepo Indicus minor, Tabern."; 8½ × 4½ cms.
8. 1591, Tabernaemontanus: "Melopepo compressus"; 12 × 7½ cms.
   1597, Gerarde: "Pepo maximus compressus"; 12 × 7½ cms.
9. 1591, Tabernaemontanus: "Melopepoteres"; 12 × 7 cms.
   1597, Gerarde: "Pepo maximus rotundus"; 12 × 7 cms.
10. 1591, Tabernaemontanus: "Pepo maximus oblongus"; 11½ × 7½ cms.
    1597, Gerarde: as above.
11. 1591, Tabernaemontanus: "Pepo Indicus minor angulosus"; 12 × 7½ cms.
    1597, Gerarde: "Pepo Indicus angulosus"; 12 × 7½ cms.
    1650, Bauhin: "Pepo Indicus minor angulosus, Tabern."; 9 × 4½ cms.; mirror image.

Cucurbita Pepo, var. *Melopepo:*

1. 1591, Tabernaemontanus: "Pepo Indicus minor clypeatus"; 12¼ × 7¼ cms.
   1597, Gerarde: "Pepo Indicus fungiformis"; 12¼ × 7¼ cms.
   1650, Bauhin: "Cucurbita clypeiformis cortice molli, et ramosa"; 8½ × 4½ cms.; mirror image.
2. 1591, Tabernaemontanus: "Cucurbita capitata"; 12 × 7½ cms.
   1597, Gerarde: "Cucurbita sylvestris fungiformis"; 12 × 7½ cms.
   1636, Gerarde: as above.
   1650, Bauhin: "Cucurbita capitata Tabernomontani sive clypeiformis"; 8½ × 4½ cms.; mirror image.
3. 1591, Tabernaemontanus: "Melopepo clypeatus"; 12½ × 7 cms.
   1597, Gerarde: "Pepo maximus clypeatus"; 12½ × 7½ cms.
   1650, Bauhin: "Cucurbita clypeiformis sive Siciliana, Melopepon latus a nonnullis vocata"; 8½ × 4½ cms.; mirror image.

Fevillea trilobata:

1. 1648, Marcgrave-Piso: "Ghandiroba vel Nhandiroba"; 8 × 14½ cms.
   1658, Piso: "Nhandiroba"; 8 × 14½ cms.

Lagenaria vulgaris:

1. 1542, Fuchs: "Cucurbita oblonga"; folio page.
   1545, Fuchs: "Cucurbita oblonga"; octavo page; mirror image.
   1563, Dodoens: "Cucurbita anguina"; 12 × 7 cms.; mirror image.
   1650, Bauhin: "Cucurbita longa, folio molli, flore albo"; 8½ × 4½ cms.
2. 1542, Fuchs: "Cucurbita maior"; folio page.
   1545, Fuchs: "Cucurbita maior"; octavo page; mirror image.
   1563, Dodoens: "Cucurbita cameraria maior"; 12 × 6½ cms.; mirror image.
   1587, Dalechamps: "Cucurbita cameraria maior"; 12 × 6½ cms.
   1636, Gerarde: "Cucurbita lagenaria"; 12 × 6½ cms.; mirror image.
   1650, Bauhin: "Cucurbita latior folio molli, flore albo"; 8½ × 5 cms.
3. 1542, Fuchs: "Cucurbita minor"; folio page.
   1545, Fuchs: "Cucurbita minor"; octavo page; mirror image.
   1563, Dodoens: "Cucurbita minor"; 12 × 7 cms.; mirror image.
   1587, Dalechamps: "Cucurbita cameraria minor"; 11½ × 6½ cms.
   1650, Bauhin: "Cucurbita lagenaria"; 8½ × 4½ cms.
4. 1576, L'Obel: "Cucurbita sive zuccha omnium maxima anguina"; 13 × 7 cms.
   1591, L'Obel: as above.
   1616, Dodoens: "Cucurbita longior"; 13 × 7 cms.
   1636, Gerarde: "Cucurbita anguina"; 13 × 7 cms.
   1640, Parkinson: "Cucurbita longa"; 13 × 7 cms.
5. 1576, L'Obel: "Cucurbita lagenaria"; 13 × 7 cms.
   1591, L'Obel: as above.
   1616, Dodoens: "Cucurbita prior"; 13 × 7 cms.
   1636, Gerarde: "Cucurbita lagenaria sylvestris"; 13 × 7 cms.
   1640, Parkinson: "Cucurbita lagenaria maior"; 13 × 7 cms.
6. 1591, Tabernaemontanus: "Cucurbita Indica minor"; 12 × 7½ cms.
   1597, Gerarde: "Cucurbita anguina"; 12 × 7½ cms.
7. 1591, Tabernaemontanus: "Cucurbita lagenaria maior"; 12½ × 7 cms.
   1597, Gerarde: "Cucurbita lagenaria"; 12½ × 7 cms.
8. 1591, Tabernaemontanus: "Cucurbita lagenaria minor"; 12 × 7¼ cms.
   1597, Gerarde: "Cucurbita lagenaria sylvestris"; 12 × 7¼ cms.

EXPLANATION OF PLATE

PLATE XI

"Pepo" *(Cucurbita Pepo)*, vol. II, pl. 33, *Institutiones rei herbariae*, Joseph Pitton de Tournefort, Paris, 1700.

ANN. MO. BOT. GARD., VOL. 48, 1961

BOTANIQUE.

DICOTYLÉDONES. Nandirobées. *Juss.*

Turpin pinx.t et direx.t *Torquati sculp.*

NANDIROBE à feuilles de lierre.

Explanation of Plate

PLATE XII

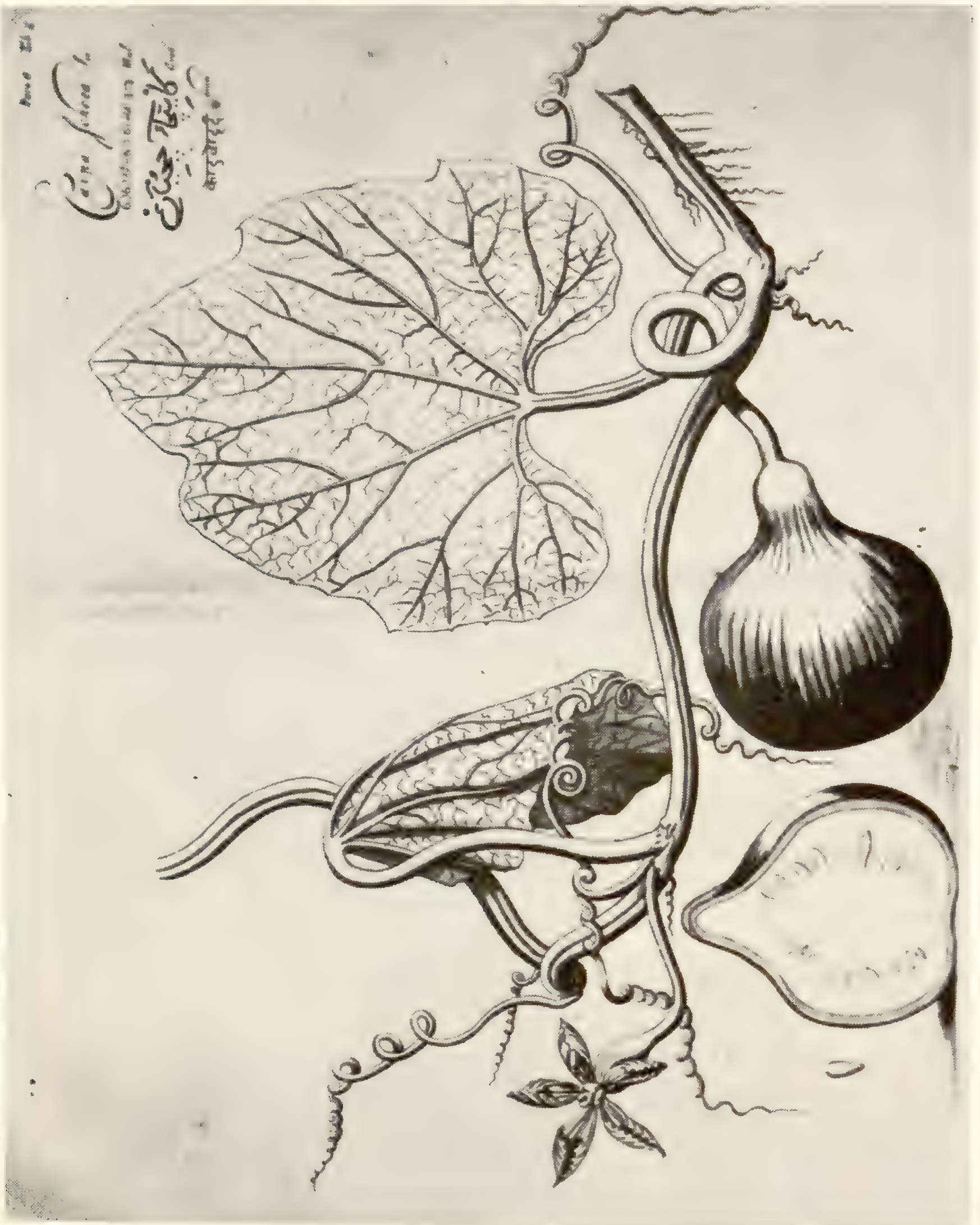
"Nandirobe à feuilles de lierre" *(Fevillea cordifolia)*, vol. LXIII, pl. 210, *Dictionnaire des Sciences Naturelles*, Paris, 1816–30.

Explanation of Plate

PLATE XIII

"Nandirobe à feuilles de lierre" *(Fevillea cordifolia)*, vol. LXIII, pl. 211, *Dictionnaire des Sciences Naturelles*, Paris, 1816–30.

NANDIROBE à feuilles de lierre.



EISENDRATH—A STUDY OF THE ICONES

Explanation of Plate

PLATE XIV

"Caipa Schora" *(Lagenaria vulgaris)*, vol. VIII, pl. 5, *Hortus Indicus Malabaricus*, Hendrik Adrian van Rheede tot Draakestein, Amsterdam, 1678–1703.

A SYNOPSIS OF POINSETTIA (EUPHORBIACEAE)

ROBERT L. DRESSLER

ABSTRACT

The position of *Poinsettia* in the tribe Euphorbieae is discussed, and a key is given for the American genera. The name *P. heterophylla* is found to be applicable to a weedy tropical plant, and the distinctions between this and the North American *P. cyathophora* are tabulated. Gametic chromosome numbers of 14 and 28 are reported for both *P. cyathophora* and *P. dentata*, while *P. heterophylla* shows only n = 14. The geographic variation of the North American annual species is briefly discussed. A key is given for the 11 species recognized, of which two are described as new: *P.* **coccinea** and *P.* **inornata**, while new combinations are published in *Poinsettia* for *P.* **colorata**, *P.* **pentadactyla** and *P.* **restiacea**. ROBERT L. DRESSLER, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

There are not many species in the genus *Poinsettia*, but their bewildering foliar polymorphism has caused a great deal of confusion. While studying the genus *Pedilanthus* (Dressler 1957), some observations were made on other genera of the tribe Euphorbieae. In the summer of 1957 I was able to observe most of the North American species of *Poinsettia* in Mexico and the southwestern United States.* Many collections made at that time have been grown and studied at the Missouri Botanical Garden. These observations have permitted considerable clarification of the annual species, especially. While I am no longer actively studying the Euphorbieae, it is felt that these notes on *Poinsettia* may be of some value.

GENERIC CONCEPT

The Linnaean genus *Euphorbia*, as it is frequently used, includes most of the tribe Euphorbieae, and is surely the most broadly inclusive generic concept in modern usage (among flowering plants). I much prefer to recognize about fourteen genera in the tribe Euphorbieae, six of these being included in the genus *Euphorbia* by many authors. I have no quarrel with those who prefer the inclusive concept of *Euphorbia*, but feel that the same arguments could be used to reduce most Compositae to *Aster*, with about equal profit. In the narrower sense, *Euphorbia* is a distinctive group of about 80 Old World species which are woody or succulent, and usually have two spines (rarely 1) near each leaf base. These spines are frequently considered to be stipular, but true stipules appear to be present in addition to the spines. The large group of south African succulents which are spineless or have spines formed from axillary branches are not directly related to the above group. The earliest generic name for the south African group is *Medusea* Haw. Neither of these groups is represented in the New World, the American succulents being members of *Agaloma* or *Tithymalus*. The largest and most difficult of the segregate genera is *Tithymalus*, which is largely an Old World group, but includes three major American groups: (1) Primitive woody species, such as *Euphorbia (Tithymalus) fulva* Stapf and *Tithymalus calyculatus* (HBK.) Kl. & Gke., of the West Indies, Central America and the Andes. (2) Herbaceous

* I am especially grateful to the Gray Herbarium and the National Science Foundation for their support of the field work in northeastern Mexico. Special thanks are also due Dr. Rogers McVaugh, who kindly lent material of *P. restiacea* which he collected, and Dr. John D. Dwyer, for aid with the Latin diagnoses.

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perennials related to *Tithymalus chrysophyllus* Kl. & Gke. and *Euphorbia (Tithymalus) floridana* Chapm. This group includes two or three species of the southeastern United States and a number of southern South America, all of them with a conspicuous pistillate calyx. (3) Herbaceous species which are closely related to Old World sorts and are surely geologically late invaders of the New World. These include *Tithymalus commutatus* (Engelm.) Kl. & Gke. and *T. campester* (Cham. & Schlecht.) Kl. & Gke., and are largely montane forms. There are also a few anomolous species which do not fall into these groups, such as *Tithymalus trichotomus* (HBK.) Kl. & Gke. and *Euphorbia (Tithymalus) pteroneura* Berger.

Most New World Euphorbieae belong to the distinctive group made up of *Agaloma, Poinsettia* and *Chamaesyce.* Of the three, *Chamaesyce* is most frequently treated as a distinct genus, while *Agaloma* generally has been kept in *Euphorbia.* These two groups are closely related, but can be distinguished by habit and by the distinctive leaf structure of *Chamaesyce.* While *Agaloma* can almost always be distinguished from *Tithymalus* by the appendaged glands, this feature is not infallible. The diminutive *Euphorbia misella* Watson, of alpine meadows in central and southern Mexico appears to lack gland appendages, but close scrutiny shows rudimentary appendages beneath the glands, indicating that it is a reduced member of *Agaloma.* Similarly, *Euphorbia heterophylla* var. *eriocarpa* Millsp. may belong in *Agaloma,* but lacks the gland appendages characteristic of that group (see excluded species, p. 340). *Agaloma* is greatly in need of monographic study, and there would be very little profit in wholesale new combinations made without such study. For this reason, I propose to cite the species of *Agaloma* as, for example, "*Euphorbia (Agaloma) corollata* L.," with the understanding that this group is quite distinct from true *Euphorbia.* The same system, of course, may be used for *Medusea,* or even *Tithymalus.* A tentative key to the New World genera of Euphorbieae is given below.

1. Leaves opposite or (rarely) ternate; the branching dichasial throughout; the veins of the leaves sheathed with chlorenchyma (usually visible by transmitted light)...Chamaesyce S. F. Gray
1. Leaves various; at least the base of the plant monopodial; leaf veins without distinct chlorenchyma sheaths. 2
2. Glands of the involucre crenate or entire, often with two lateral horns, but without distinct petaloid appendages....3
3. Glands of the involucre 4 or 5, not cup-like or bilabiate....Tithymalus Trew
3. Glands usually 1 or 2, cup-like, bilabiate, or shield-like....4
4. The involucral lobes connate to their apices; two glands united into a lateral shield-like structure; the cymes pseudo-umbellate; the pistillate flowers calyculate.... ....Cubanthus Millsp.
4. The involucral lobes apically distinct; the gland cup-like or bilabiate; inflorescence a condensed pleiochasium or dichasium, the branches becoming monochasial; the pistillate flower naked....Poinsettia Grah.
2. Glands of the involucre with distinct petaloid appendages, these often laciniate....5
5. The involucral lobes equal; the gland appendages not forming a single hood-like spur. ....Agaloma Raf.
5. The involucre highly zygomorphic, with 2 large lobes and 3 very small ones; the gland appendages forming a spur on one side of the involucre....Pedilanthus Neck.

Generic Relationships

As noted above, *Poinsettia* is closely allied to *Agaloma,* though readily distinguished by the lack of petaloid appendages on the glands. *Euphorbia (Agaloma) lancifolia* Schlecht. is especially similar to *Poinsettia,* and resembles that genus in

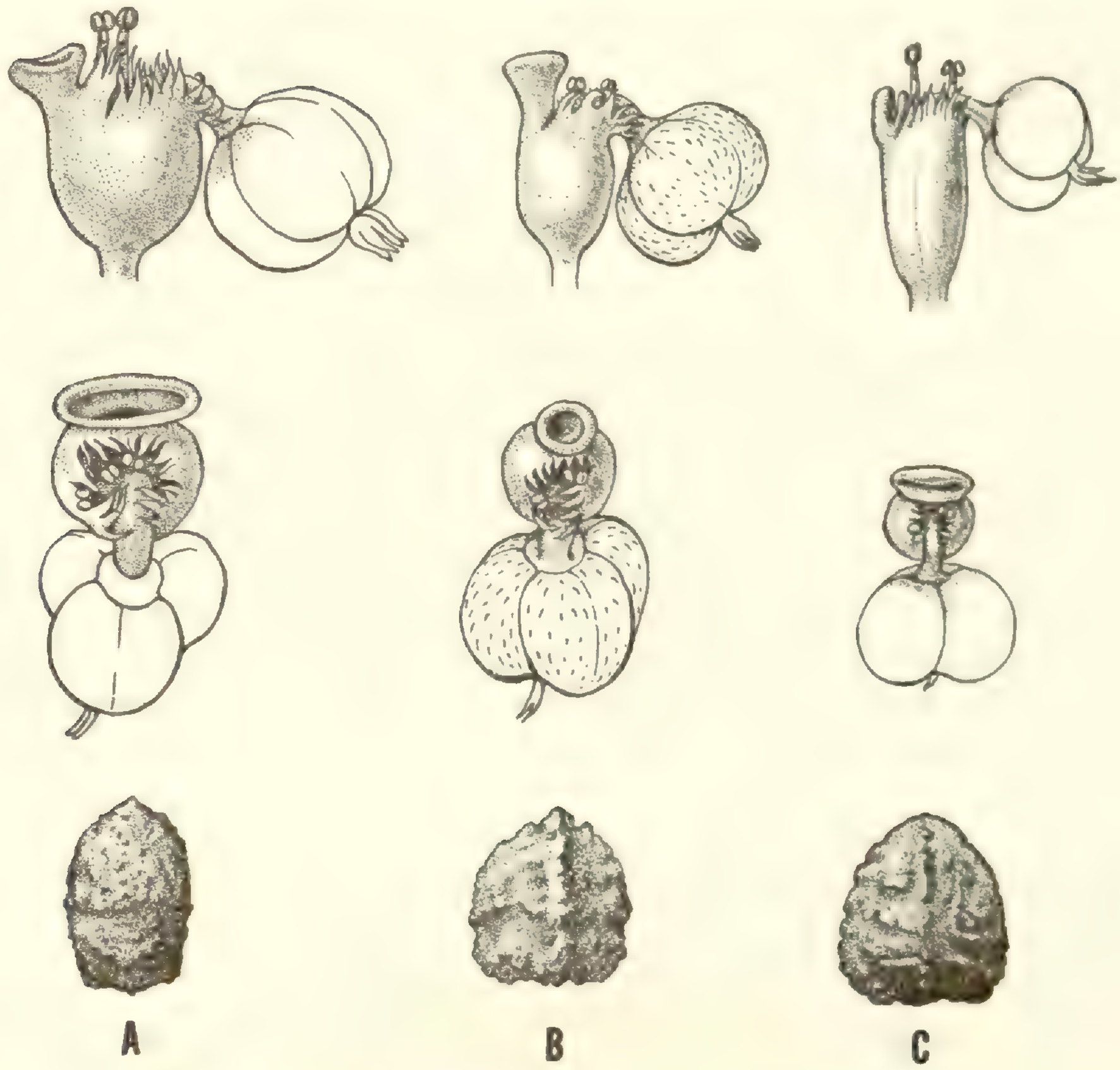

Figure 1. Cyathia and seed of the North American annual poinsettias. A. *P. cyathophora* (Dressler 2430), B. *P. heterophylla* (Dressler 2254), C. *P. dentata* (Dressler 2198). Above: side view of cyathium, ×5; middle: top view of cyathium, ×5; below: dorsal view of seed, ×7.5. All drawn from fresh, living specimens.

habit, in the tendency toward reduced gland number, in the form of the glands, in the reduced petaloid appendages and in the thick-walled, coarsely reticulate pollen grains. The seed of *E. (A.) lancifolia* is very different from that of *Poinsettia*, which serves to reinforce the generic distinction. Several other species of *Agaloma* have been confused with *Poinsettia*, though they are less closely related (see excluded species, p. 340). *Poinsettia* is evidently derived from *Agaloma* by the loss of petaloid appendages and reduction in number of glands. While the involucre of *Poinsettia* generally has only a single gland, the central involucre of a pleiochasium, especially, is likely to have a full complement of five glands.

The Identity of Euphorbia heterophylla L.

Much of the confusion concerning the annual poinsettias has centered about the identity of Linnaeus' *Euphorbia heterophylla*. The epithet seems very descriptive of the familiar North American plant with red and green floral bracts, and most botanists seem to have assumed that it applied to this plant. One finds, though, that Linnaeus' epithet refers to the *shape* of the leaves, rather than to their color.

There is no specimen of *E. heterophylla* in the Linnaean herbarium, so one must turn to *Tithymalus curassavicus, salicis & atriplicis foliis varius, caulibus viridantibus* of Plukenet's Almagestum Botanicum (1696). Plukenet's figure shows a plant with both lanceolate and pandurate leaves, quite characteristic of the weedy tropical species with green floral bracts. Leaf shape is none too dependable in this group, but the entire lanceolate form shown is rarely encountered in the North American *P. cyathophora.* It is conceivable, of course, that the North American ornamental had been introduced into Curaçao by that date, but it is hardly likely that Plukenet would have failed to mention the red floral bracts of that species.

It should not be concluded that Linnaeus' epithet has been consistently and discerningly misapplied to the North American species. Rather, most specimens of either species from North and Central America have been determined as *E. heterophylla,* while South American specimens of true *E. heterophylla* have more often been labeled as *E. geniculata* or *E. elliptica.* The consistent confusion of these two species is based on very superficial observation, for the two differ from each other much more than either differs from *P. dentata,* which is generally recognized as distinct. A tabular comparison of the two species is given herewith.

Poinsettia cyathophora	Poinsettia heterophylla
Stems and petioles glabrous or sparsely pilose.	Stems and petioles often markedly pilose.
Leaves glossy green.	Leaves dull green.
Floral bracts usually basally red.	Floral bracts green or basally pale, never basally red (often purple spotted).
Gland broad, more or less bilabiate, the opening narrowly oblong.	Gland narrow, substipitate, the opening circular.
Seed finely and sharply tuberculate, not angular.	Seed coarsely and bluntly tuberculate, angular.

Chromosome Number

A number of chromosome counts have been made from material cultivated at Missouri Botanical Garden. These are given below, with the counts previously published by Perry (1943). Voucher specimens are available for all those which have collection numbers.

Poinsettia cyathophora	Gametic No.	Somatic No.
Dressler 1821 (Tamaulipas)	14	
Dressler 2271 (Tamaulipas)	14	
Dressler 2430 (Nuevo León)	14	
s. n. Washington, Missouri	14	
s. n. Grey Summit, Missouri	14	
Dressler 2373 (Tamaulipas)	28	
Cultivated (Rex Pearce)	28	
Cultivated (Parke)	28	
Perry (cult. as *Euphorbia heterophylla*)		56

Poinsettia dentata	Gametic No.	Somatic No.
Dressler 2268 (Oaxaca)	14	
s. n. Grey Summit, Missouri	14	
Dressler 2198 (Texas)	28	
s. n. Empalme Escobedo, Guanajuato	28	
Perry, Clarke Co., Virginia		14, 28
Davis, Oklahoma		28
Pleasant Hill, Missouri		56

Poinsettia heterophylla	Gametic No.	Somatic No.
Dressler 2136 (Tamaulipas)	14	
Dressler 2194 (Arizona)	14	
Dressler 2243 (Vera Cruz)	14	
Howard & Proctor 13883 (Jamaica)	14	
Manning & Manning 531217 (Jalisco)	14	
s. n. Soledad, Cuba	14	
Moyer (cited by Perry) as *E. geniculata*		28

Poinsettia pulcherrima	Somatic No.
Perry	28

From the above counts, one could consider 14 to be the base number for the genus, if it were not for Perry's record of a somatic number of 14 for one plant of *P. dentata*. It is at least conceivable that the plant studied by Perry was a chance haploid, but more counts are needed from the eastern United States, before this can be evaluated properly. There is no indication of polyploidy in *P. heterophylla*, but *P. cyathophora* and *P. dentata* both contain polyploids. These are discussed further in the next section.

Patterns of Variation

The most outstanding feature of the annual species of *Poinsettia* is their extreme polymorphism. Linear-lanceolate, ovate and deeply pandurate leaves may be found not only in the same population, but on the same individual. More frequently, however, extremely different leaf types are found on different individuals or on different stages of one individual. It would appear that there is an interaction of genetic and environmental control in such cases. The perennial species are less markedly polymorphic, but all of the adequately sampled species show some degree of foliar polymorphism. Even seed structure shows a good deal of variation in *Poinsettia*, though this feature is usually dependably stable in the Euphorbieae.

In spite of the extreme polymorphism, some patterns of geographic or genetic variation are evident, and merit more detailed study.

1. *Poinsettia cyathophora.* This species is perhaps the most highly variable of the genus. The cultivated polyploids ($n = 28$) are coarse, somewhat weedy plants that show little polymorphism, and have somewhat coriaceous leaves. When collected in a dry, rocky arroyo, the plants of *Dressler 2373* were relatively small, but when cultivated in St. Louis, they became large and coarse, very closely resembling the cultivated plants of the same chromosome number. Many of the more delicate

plants of lower chromosome number would seem to have greater ornamental potential than the polyploids now available.

Collections from Oaxaca and Nuevo León have behaved as distinctly short-day plants, while one collection from Tamaulipas (Rancho del Cielo) has proven to be relatively day-neutral. The characteristic red bracts of this species are a surprisingly dependable key feature, but some plants of the Missouri Ozarks lack the red coloring.

2. *Poinsettia dentata.* This species shows a good deal of geographic variation, which is complicated by polyploidy. The plants with n = 14 of southern Mexico are much branched and often decumbent, strongly pilose plants with very condensed, nearly capitate inflorescence and cream or yellowish floral bracts. This is apparently the form described as *Poinsettia schiedeana.* These features become less marked to the north, suggesting a clinal pattern. One also finds erect, rather weedy plants with little or no bract coloration in Mexico. These are frequent in disturbed areas of central Mexico, and closely resemble the forms of this species which grow in Arizona and western Texas. It is probable that these weedy forms have entered Mexico from the north and are genetically isolated from the native form by their higher chromosome number.

Some of the semi-desert forms from northern Mexico are striking because of their small, coriaceous leaves. The type of Engelmann's var. *rigidia* is not the extreme in this feature.

3. *Poinsettia heterophylla.* This tropical species shows less variation than its temperate counterparts. Occasional populations with whitish floral bracts, strongly dentate leaves or very pilose stems suggest introgression from *P. dentata,* and I suspect that these two do hybridize to a certain degree where *P. heterophylla* grows with a population of *P. dentata* having the same chromosome number.

Taxonomy

Poinsettia Graham, Edinb. New Philos. Jour. 20:412. 1836. Type: *Euphorbia pulcherrima* Willd.

Pleuradena Raf., Atl. Jour. 1(6):182. 1833, not *Pleuradenia* Raf., 1825. Type: *Pleuradena coccinea* Raf.

Cyathophora Raf., Fl. Tell. 4:117. 1838, not *Cyathophora* S. F. Gray, 1821. Type: *Euphorbia heterophylla* L.

Woody or herbaceous, often perennial from a fleshy storage root; leaves alternate or opposite, stipules inconspicuous or absent, appearing glandular; inflorescence a condensed pleiochasium or dichasium, the branches becoming monochasial; involucral glands more or less cup-like, usually reduced in number (commonly 1); pollen grains thick-walled and coarsely reticulate; pistillate flower naked.

Key to Species

1. Plants woody, or perennial from thickened storage roots.....2
   2. Woody plants, generally exceeding 2 meters in height; involucre usually more than 5 mm. in diameter; seeds ca. 10 mm. long.....1. P. pulcherrima
   2. Herbaceous plants, less than 1 meter tall; involucre usually less than 5 mm. in diameter; seeds 2–5 mm. long.....3

3. Plant ca. 1 dm. tall, flowering on short leafless stems, the vegetative stems developing later, usually more or less decumbent.....2. P. RADIANS
3. Plants 2–5 dm. tall; foliage and flowers borne on same stem, stems erect.....4
4. Floral bracts white; glands white, with the outer rim flaring and somewhat petaloid (western Mexico).....3. P. RESTIACEA
4. Floral bracts red or red and green; glands red, yellow or green, the outer rim not flaring and petaloid.....5
5. Leaves entire, markedly paler beneath (northwestern Mexico).....5. P. COLORATA
5. Leaves more or less serrate, not markedly paler beneath.....6
6. Foliage markedly scabrous-strigose; gland broadly campanulate, the inner and outer rims similar; seed 3–4 mm. long (western Mexico).....4. P. STRIGOSA
6. Foliage subglabrous; gland narrow, the outer rim much thicker than the inner; seed 2–2.5 mm. long (northeastern Mexico).....6. P. COCCINEA
1. Plants annual, without thickened storage roots.....7
7. Style branches (3) entire, about one half connate, much longer than the ovary (Paraguay and Argentina).....9. P. PENTADACTYLA
7. Style branches divided, not longer than the ovary.....8
8. Seeds smooth, with an equatorial row of blunt tubercles and one or two fainter rows; low spreading, delicate plant (Peru).....10. P. INORNATA
8. Seeds strongly tuberculate; generally coarser, erect plants.....9
9. Glands more or less funnel-like, the opening circular; coarse tropical weed.....11. P. HETEROPHYLLA
9. Glands more or less bilabiate, the opening narrowly oblong.....10
10. Lower leaves usually alternate; floral bracts usually basally red; seeds without caruncle (North America).....7. P. CYATHOPHORA
10. All leaves usually opposite; floral bracts green or cream at base, sometimes with purple spots, but never basally red; seeds often carunculate.....11
11. Seeds finely and sharply tuberculate (North America).....8. P. DENTATA
11. Seeds coarsely and bluntly tuberculate (Argentina).....P. species*

1. POINSETTIA PULCHERRIMA (Willd.) Grah., Edinb. New Philos. Jour. 20:412. 1836.

Euphorbia pulcherrima Willd. ex Klotzsch, Allg. Gartenz. 2:27. 1834.
Pleuradena coccinea Raf., Atl. Jour. 1(6):182. 1833, not *Poinsettia coccinea* Dressler
Euphorbia erythrophylla Bertol., Nov. Comment. Acad. Scient. Inst. Bonon. 4:419, t. 41. 1840.
Euphorbia fastuosa Sessé & Mociño, Pl. Nov. Hisp. 81. 1888.

Distribution. The familiar cultivated poinsettia occurs as a wild plant in the rocky canyons of western Mexico, in Nayarit, Jalisco and Colima. Dr. Rzedowski suggests (personal communication) that it may also occur further south, in Michoacan and Guerrero. The habit of the plant, with a fleshy storage root especially well developed in the seedling stage, is characteristic of the tropical deciduous forest of this area.

2. POINSETTIA RADIANS (Benth.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859.

Euphorbia radians Benth., Pl. Hartw. 8. 1839.
Euphorbia stormiae Croiz., Rev. Sudam. Bot. 6:13. 1939 [Type: *Storm s. n.* AH!].

Distribution. Arizona through central Mexico to Oaxaca.

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* Several Argentine specimens may represent an undescribed species. Some of these were determined by Croizat as *Euphorbia aureocincta* Croiz., but that epithet is irrevocably typified by a specimen of *P. heterophylla*. The plants in question are very similar to *P. dentata*, but differ somewhat in seed structure, and possibly in the proportions of the involucre. More material and study are needed to fix the status of these plants, so they shall remain nameless for the present. They are *Castellano s. n.* Dec. 5, 1927 (GH), *Castillón 1851* (GH), *Meyer 3647* (GH) and *Schreiter 10990* (AAH).

3. Poinsettia **restiacea** (Benth.) comb. nov.

Euphorbia restiacea Benth., Bot. Voy. Sulph. 162. 1844.

Distribution. Western Mexico (Nayarit and Durango).

Superficially the plants of *P. restiacea* resemble some species of *Agaloma*, such as *Euphorbia sphaerorhiza* Benth., because of the slender stems, narrow white bracts and conspicuous white glands. Though the outer rim of the gland is flattened and somewhat petaloid, there is no sharp distinction between gland and appendage, such as characterizes the members of *Agaloma*. The type specimen (K) is very scrappy, but a photograph (MICH) indicates that it is probably the same species as the excellent material which Dr. McVaugh has collected in Nayarit.

4. Poinsettia strigosa (Hook. & Arn.) Arthur, Torreya 11:260. 1912.

Euphorbia strigosa Hook. & Arn., Bot. Voy. Beech. 310. 1840.
Poinsettia pedunculata Klotzsch, Seem. Bot. Voy. Herald 277. 1856.

Distribution. Western Mexico (Nayarit and Jalisco).

5. Poinsettia **colorata** (Engelm.) comb. nov.

Euphorbia colorata Engelm., Rep. U. S. & Mex. Bound. Surv. 2:190. 1859 [Type: *Thurber 265*, GH!].
Euphorbia tuberosa Rose, Contr. U. S. Nat. Herb. 1:111. 1891, not *E. tuberosa* L., 1753.

Distribution. Northwestern Mexico (Sinaloa, Sonora and Zacatecas).

6. Poinsettia **coccinea** sp. nov. Figure 2

Perennis, erecta, 40–70 cm. alta, radice tuberosa oriens, caulibus basi lignescentibus, glabris; folia alterna, linearia vel anguste lanceolata, 1.5–6 mm. lata, 40–120 mm. longa, subtus hispidula, ad basin barbellata, apice attenuata, basi attenuata vel breviter petiolata, marginibus serratis vel subintegris; cymarum bracteae coloratae, lineari-lanceolatae vel elliptico-lanceolatae, 3.5–7 mm. latae, 30–80 mm. longae; inflorescentiae compactae; involucra anguste campanulata, 3–3.5 mm. lata, 3.5–4 mm. longa, glandulis involucrum excedentibus, 1.5–2 mm. latis, marginibus externis crassioribus altioribusque; ovarium glabrum; styli ca. 1 mm. longi, basi breve connati, fere ad medium bipartiti; semina oblongo-ovoidea, ecarunculata, tuberculata, ca. 2.5 mm. longa.

Mexico. tamaulipas, Municipio de Aldama, Sierra de Tamaulipas, above Juan Tomás, east of Rancho Las Yucas (ca. 40 km. nnw. of Aldama). Oak scrub and rocky arroyo, October 13, 1957, bracts basally red, roots with series of thickened "tubers," *R. L. Dressler 2395* (Type: MO, isotypes to be distributed). Other collections from the same region are: Las Yucas, Oak scrub (chaparral), peak of Cerro de Las Yucas, July 20, 1957, rocky soil, *R. L. Dressler 1930* (MO); near Paso Lajas (Ejido Las Yucas), Oak scrub, October 10, 1957, *R. L. Dressler 2343* (GH). nuevo león, Rancho Resendez, Lampazos, June 22, 1937, "Pico de perico," *M. T. Edwards 313* (MO, incomplete, but apparently this species).

This species is related to *P. colorata*, but may be distinguished by the usually serrate leaves which are not markedly paler beneath and by the smaller green (rather than red) cyathia; the gland also is smaller and differently shaped. *Poinsettia coccinea* will more often be confused with the annual *P. cyathophora*. Under favorable conditions *P. cyathophora* may survive for two or more seasons, but it is

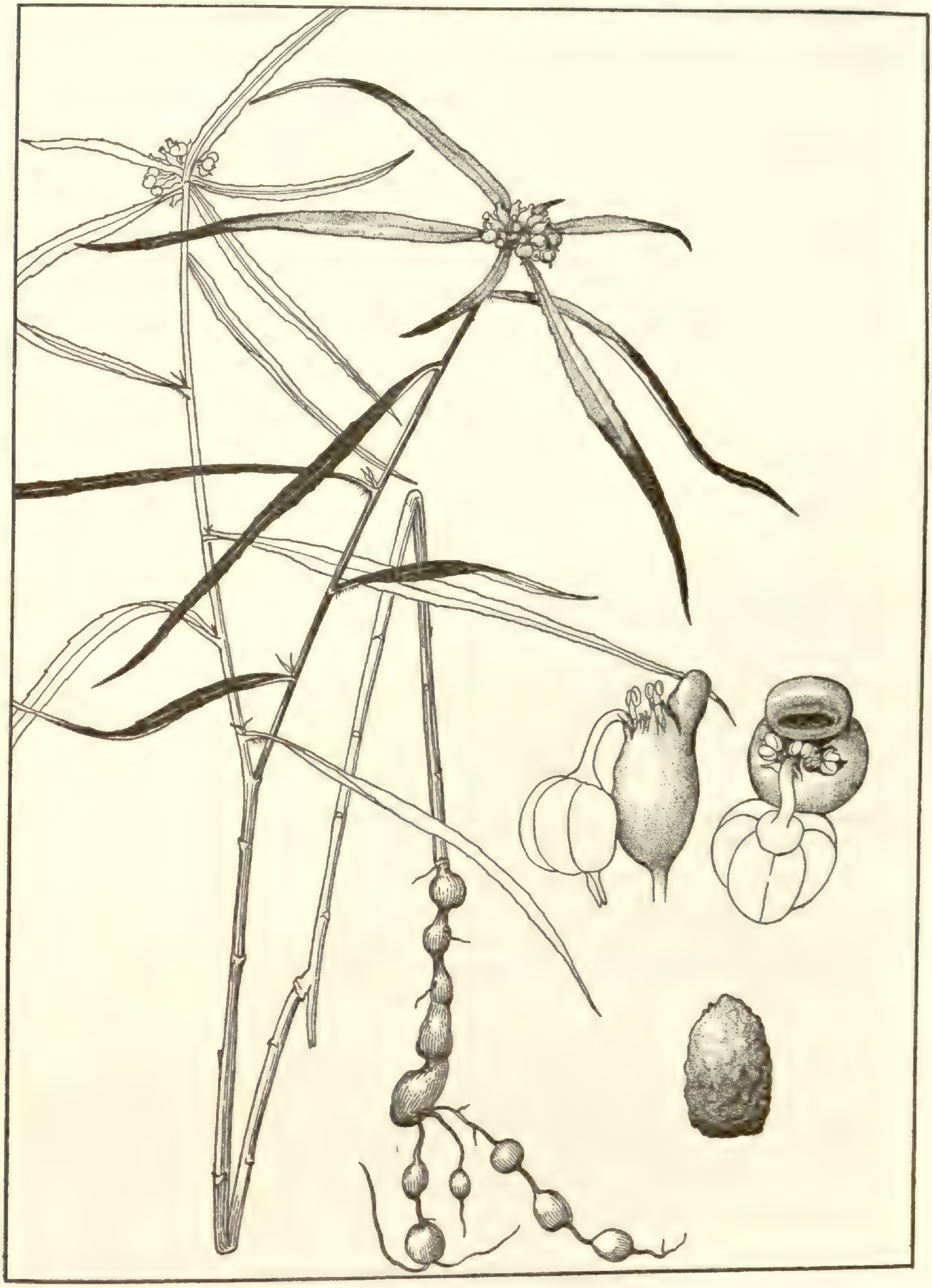

Figure 2. *Poinsettia coccinea*, drawn from living material of the type collection. Habit ×½, side view of cyathium ×5, top view ×6, dorsal view of seed ×7.5.

not known to form the fleshy "sausage-string" roots of *P. coccinea*. *Crutchfield & Johnston 5611A*, from near Jaumave, Tamaulipas, is definitely a perennial, but appears to be *P. cyathophora* (no roots were present on the specimen seen).

Poinsettia coccinea is frequent in rocky oak scrub and open oak forest in the region of the type locality. In this area it is quite distinct from *P. cyathophora*, which was found only in the polyploid form (n = 28). To the north of the Sierra de Tamaulipas other forms of *P. cyathophora* occur (*Crutchfield, Johnston & McMillan 6082, Graham & Johnston 4695*, both near Padilla, Tamaulipas), and it is quite possible that introgression may occur between the annual and perennial species in this region. No satisfactory chromosome counts have been obtained for this species, but the slides which were made indicated approximately 12 to 15 chromosomes, so this probably has n = 14.

7. Poinsettia cyathophora (Murr.) Kl. & Gke., Monatsb. Akad. Berlin 1859: 253. 1859.

Euphorbia cyathophora Murr., Comm. Götting. 7:81. 1786. *Tithymalus cyathophorus* (Murr.) Moench, Meth. 667. 1794. *Euphorbia heterophylla* β *cyathophora* (Murr.) Boiss., DC. Prod. 15(2):72. 1862. *Euphorbia heterophylla* forma *cyathophora* (Murr.) Voss, Vilmorin, Blumengärtn. (ed. 3) 1:898. 1895.
Euphorbia graminifolia Michx., Fl. Bor.-Am. 2:210. 1803. *Poinsettia graminifolia* (Michx.) Millsp., Field Mus. Pub. Bot. 2:304. 1909.
Cyathophora picta Raf., Fl. Tell. 4:117. 1838.
Cyathophora ciliata Raf., Fl. Tell. 4:117. 1838.
Euphorbia barbellata Engelm., Rep. U. S. & Mex. Bound. Surv. 2:190. 1859 [Type: *Wright s. n.*, GH!]. *Euphorbia heterophylla* var. *barbellata* (Engelm.) Holzinger, Contrib. U. S. Nat. Herb. 1:216. 1892. *Poinsettia barbellata* (Engelm.) Small, Fl. Southeastern U. S. 722, 1334. 1903.
Euphorbia heterophylla var. *graminifolia* Engelm., Rep. U. S. & Mex. Bound. Surv. 2:190. 1859.
Poinsettia edwardsii Kl. & Gke., Abh. Akad. Berlin Phys. 1859:104. 1860.
Poinsettia pinetorum Small, Fl. Miami 111, 200. 1913.

Distribution. The eastern United States south through eastern Mexico to the Isthmus of Tehuantepec; west to Colima in Mexico. Possibly native in the Greater Antilles. Widely cultivated and often naturalized.

There is a specimen from the Göttingen Botanical Garden (1794) in the Missouri Botanical Garden herbarium. While this was prepared after the description of *Euphorbia cyathophora*, it probably represents the population described by Murray.

Though this species is usually an annual, clonal material is easy to maintain by cuttings, which should facilitate the experimental study of its polymorphism. Under favorable conditions it may be a facultative perennial. I have seen specimens from northeastern Mexico and southern Florida which had over-wintered at least one season before collection.

8. Poinsettia dentata (Michx.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859.

Euphorbia dentata Michx., Fl. Bor.-Am. 2:211. 1803. *Anisophyllum dentatum* (Michx.) Haw., Syn. Pl. Succ. 162. 1812.
Euphorbia herronii Riddell, Syn. Fl. W. States 32. 1835.

Euphorbia dentata β *rigidia* Engelm., Rep. U. S. & Mex. Bound. Surv. 2:190. 1859 [Type: *Wright 1837*, MO!].
Euphorbia dentata γ *cuphosperma* Engelm., Rep. U. S. & Mex. Bound. Surv. 2:190. 1859 [Type: *Wright 1834*, MO!]. *Euphorbia cuphosperma* (Engelm.) Boiss., DC. Prod. 15(2):73. 1862. *Poinsettia cuphosperma* (Engelm.) Small, Fl. Southeastern U. S. 721, 1334. 1903. *Euphorbia dentata* forma *cuphosperma* (Engelm.) Fern., Rhodora 50:148. 1948.
Poinsettia schiedeana Kl. & Gke., Abh. Akad. Berlin Phys. 1859:102. 1860.
Euphorbia dentata β *lasiocarpa* Boiss., DC. Prod. 15(2):72. 1862.
Euphorbia dentata γ *linearis* Engelm. ex. Boiss., DC. Prod. 15(2):72. 1862.
Euphorbia dentata var. *gracillima* Millsp., Pittonia 2:90. 1890.
Euphorbia dentata var. *lancifolia* Farwell, Am. Midl. Nat. 8:273. 1923.

Distribution. The eastern United States west to Arizona and south through Mexico possibly to Guatemala. To be expected as a weed elsewhere.

9. Poinsettia **pentadactyla** (Griseb.) comb. nov.

Euphorbia pentadactyla Griseb., Gött. Abh. 24:63. 1879.

Distribution. Paraguay and northern Argentina.

10. Poinsettia **inornata** sp. nov. Figure 3

Annua, ramosa, 8–14 cm. alta, ramisque procumbens ad 12 cm. longa, caulibus sparse pilosis; folia alterna vel ea basalia opposita, ovata vel elliptica, 8–16 mm. lata, 12–32 mm. longa, subtus sparse hispidula, apice acuta, basi cuneata, marginibus leviter serratis et hispidulis, petiolis 2–6 mm. longis; cymae dichotomae, involucris late campanulatis, ca. 2 mm. longis, 1.2–2 mm. latis, glandulis 0.6–0.8 mm. latis, ostio oblongo; ovarium glabrum styli ca. 1 mm. longi, basi breve connati, fere ad basin bipartiti; semina quadrato-ovoidea, minute carunculata, sub-laevia, paucituberculata, 2.5 mm. longa.

Peru. Dept. & Prov. Lima, Dist. Pachacamac; Atacongo; among rocks in arid valley, alt. 195 m., common, scattered, October 14, 1935, *Ynes Mexia 04044* (Type: MO, isotype GH, presumably also at UC).

This is apparently a deep-rooted, spreading annual. The plant would pass superficially for a small delicate *P. heterophylla*, but the gland is quite different in shape, and the nearly smooth seed with an equatorial row of small, blunt tubercles, and fainter basal and distal rows, is unlike that of any other species of *Poinsettia*.

11. Poinsettia heterophylla (L.) Kl. & Gke., Monatsb. Akad. Berlin 1859: 253. 1859.

Euphorbia heterophylla L., Sp. Pl. 453. 1753. *Tithymalus heterophyllus* (L.) Haw., Syn. Pl. Succ. 141. 1812. *Cyathophora heterophylla* (L.) Raf., Fl. Tell. 4:117. 1838.
?*Euphorbia elliptica* Lam., Encyc. Meth. Bot. 2:425. 1788. *Euphorbia heterophylla* var. *elliptica* (Lam.) O. Ktze., Rev. Gen. 2:605. 1891.
?*Euphorbia linifolia* Vahl, Symb. Bot. 2:53. 1791. *Euphorbia heterophylla* var. *linifolia* (Vahl) O. Ktze., Rev. Gen. 2:605. 1891.
Euphorbia geniculata Ortega, Hort. Mat. Dec. 18. 1797. *Poinsettia geniculata* (Ort.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859. *Euphorbia heterophylla* ε *geniculata* (Ort.) Gómez, Anal. Hist. Nat. Madrid 23:46. 1894.
Euphorbia prunifolia Jacq., Hort. Schoenb. 3:15, t. 277. 1798. *Tithymalus prunifolius* (Jacq.) Haw., Syn. Pl. Succ. 143. 1812. *Poinsettia prunifolia* (Jacq.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859.

Euphorbia frangulaefolia HBK., Nov. Gen. et Sp. 2:62. 1817. *Poinsettia frangulaefolia* (HBK.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859.
Euphorbia trachyphylla A. Rich., La Sagra, Hist. Cuba 9:198. 1850.
Euphorbia morisoniana Kl., Seem. Bot. Voy. Herald 100. 1853. *Poinsettia morisoniana* (Kl.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859.
Poinsettia ruiziana Kl. & Gke., Abh. Akad. Berlin Phys. 1859:102. 1860.
?*Euphorbia heterophylla* δ *minor* Boiss., DC. Prod. 15(2):73. 1862.
Euphorbia heterophylla var. *brasiliensis* Müll. Arg., Mart. Fl. Bras. 11(2):695. 1874.
Euphorbia prunifolia var. α *repanda* Müll. Arg., Mart. Fl. Bras. 11(2):694. 1874.
Euphorbia prunifolia var. γ *angustifolia* Müll. Arg., Mart. Fl. Bras. 11(2):695. 1874.
Euphorbia zonosperma Müll. Arg., Mart. Fl. Bras. 11(2):696. 1874.
Euphorbia heterophylla β *elliptica* forma *hirticaulis* O. Ktze., Rev. Gen. 3(2):286. 1898.
Poinsettia havanensis Small, Fl. Southeastern U. S. 722, 1334. 1903.
Euphorbia aureocincta Croiz., Jour. Arnold Arb. 24:181. 1943 [Type: *Rojas 3379*, AH!].

Distribution. From Arizona and Tamaulipas southward throughout the American tropics. As a weed throughout the tropics. Naturalized in Louisiana and Texas and to be expected elsewhere.

Excluded Species

Poinsettia eriantha (Benth.) Rose & Standley, Contrib. U. S. Nat. Herb. 16:13. 1912. = *Euphorbia (Agaloma) eriantha* Benth. This species, *E. (A.) exstipulata* Engelm., *E. (A.) jaliscensis* Rob. & Greenm., and *E. (A.) lacera* Boiss. are all closely related. All of these species have small but distinct petaloid appendages on the glands and have seeds which are unlike those of *Poinsettia*. In *E. (A.) eriantha*, at least, the pollen grains are very unlike those of *Poinsettia*.

Euphorbia heterophylla var. *eriocarpa* Millsp., Proc. Cal. Acad. II 2:230. 1889. The type (F!) is not a *Poinsettia*, but appears to be an *Agaloma* with reduced gland appendages, or possibly a *Tithymalus*. It is probably unnamed as a species.

Poinsettia insulana (Vell.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859. = *Euphorbia (Agaloma) insulana* Vell. This and the following two species are closely related, if not conspecific.

Poinsettia lancifolia (Schlecht.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859. = *Euphorbia (Agaloma) lancifolia* (Schlecht.)

Poinsettia oerstediana Kl. & Gke., Abh. Akad. Berlin Phys. 1859:103. 1860. = *Euphorbia (Agaloma) oerstediana* (Kl. & Gke.) Boiss.

Poinsettia punicea (Sw.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859. = *Tithymalus puniceus* (Sw.) Haw.

Poinsettia xalapensis (HBK.) Kl. & Gke., Monatsb. Akad. Berlin 1859:253. 1859. = *Euphorbia (Agaloma) xalapensis* HBK.

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Perry, B. A. 1943. Chromosome Number and Phylogenetic Relationships in the Euphorbiaceae. Amer. Jour. Bot. 30:527–543.
Plukenet, L. 1696. Almagestum Botanicum. London, 402 pp.
Wheeler, L. C. 1943. The Genera of the Living Euphorbieae. Amer. Midl. Nat. 30:456–503.

Figure 3. *Poinsettia inornata*, drawn from the type specimen. Habit ×3/5, cyathium ×10, dorsal view of seed ×8.

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